# POTENTIAL IMPACTS OF GLOBAL AND REGIONAL ENVIRONMENTAL CHANGES ON AN ENDANGERED POLLINATION CORRIDOR IN MEXICO AND THE USA

A Dissertation

by

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ABSTRACT

Maintaining migratory corridors that allow winged pollinators to move and transport pollen is critical for preserving the genetic diversity of plant species and, as a result maintains the resilience of the ecosystem to changes in the environment. Migratory pollinators require a tight synchrony between the timing of their migration and the peak nectar availability of flowering plants along the corridors they travel. This synchrony can easily be disrupted by climate change or by human-induced land cover change. Pollinating bats are large-bodied and can carry large pollen loads between distant populations of plants. Plants of the genus *Agave* subgenus *Agave* have evolved particular flower characteristics to attract bats. The nectar-feeding Mexican long-nosed bat (*Leptonycteris nivalis*) relies on the presence of flowering *Agave* spp. for its migration from central Mexico to the southwestern United States. *L. nivalis* is listed as endangered by the United States, Mexico and the International Union for the Conservation of Nature, due to declines in its populations of over 50% in the past ten years.

I conducted three studies to address important ecological questions related to the *Agave-L. nivalis* corridor. First, I used species distribution modeling algorithms to generate potential distributions of the *Agave* species that occur in the corridor. I created a map of *Agave* richness and analyzed the correspondence of different levels of richness with the known areas of presence of *L. nivalis*. The results indicate a relationship between occurrence of *L. nivalis* and areas with two or more *Agave* species and highlights areas along the mountain chains as the stepping-stones of the corridor.

Second, I modeled the potential distribution of the *Agave* species and *L. nivalis* under future climate scenarios for 2050 and 2070. The models indicate a significant reduction in the overlap of *Agave* spp. and *L. nivalis*. Lastly, I analyzed the effects of three decades of land cover change on *Agave* habitat. The results show that the fragmentation trend in agave habitat has slowed down from 1985 to 2011. However, even under scenarios of no further habitat loss, climate change will continue to have impacts on this plant-pollinator interaction.

# DEDICATION

To my dearest daughter Ariana, the greatest motivation in my life.

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TABLE OF CONTENTS

Page

LIST OF FIGURES

LIST OF TABLES

# CHAPTER I

# INTRODUCTION

For more than a century conservation biologists have been concerned with the conservation of migratory animals, but the understanding of the causes and consequences of changes in migrant populations continues to undergo considerable revision (Bauer and Hoye 2014). Migratory pollinators require a tight synchrony between the timing of their migration and the peak nectar availability of flowering plants along the corridors they travel (Fleming and Eby 2003). This synchrony can easily be disrupted by climate change or by human-induced land cover change.

Migratory corridors for winged pollinators have been described as a mosaic of stepping-stones within a larger matrix, with each stone as a stopover that migrants use for "refueling" while in transit along their flyways; and the "glue" providing the connectivity in this mosaic is the shared presence of certain flowering plant genera that the mobile pollinators forage if in bloom (Nabhan 2004). The concept of nectar corridors, suggested by bat ecologist Donna Howell (1974), is a sequence of flowering plants situated in each stepping-stone along a migration route. It has been observed that clusters of bat-pollinated plants bloom sequentially from south to north, creating the effect of a blooming wave. A nectar corridor is now envisioned to be the entire circulation pattern that pollinators follow as they migrate from one sequentially blooming plant population to the next (Fleming 2003).

Winged pollinators, such as nectarivorous bats, hummingbirds, doves, bees, butterflies, and moths, facilitate pollen and gene flow over considerable distances. The reproductive fitness of a plant depends substantially on the number of pollen grains transferred. An effective pollinator is able to transport the most pollen grains possible. Bats are large-bodied and can carry large pollen loads, and some plants have developed flowers with particular characteristics to attract them (Fenster et al. 2004). This flower syndrome is called chiropterophily, and it is particularly found on plants of the genus *Agave* subgenus *Agave* (hereafter 'agaves').

Agaves' geographic center of origin is Mexico. Historically, these plants have provided food and cultural services to humans in the form of natural fibers, and traditional beverages, such as tequila and mezcal (Gentry 1982). Agaves are considered keystone species in semiarid to arid regions because they play a critical role in maintaining soil stability (Gonzalez Elizondo et al. 2009).

Agave distribution is largely coincident with the distribution of nectarivorous bats. Studies suggest that the increase in speciation in agaves was precipitated by their colonization to arid environments and that particularly two species of bats specialized for nectar feeding (*Leptonycteris nivalis* and *L. yerbabuenae*) played an important part in this process (Good-Avila et al. 2006, Rocha et al. 2006).

I focused this dissertation on the nectar trail of agaves that *L. nivalis* follows for its migration. The Mexican long-nosed bat (*Leptonycteris nivalis,* family Phyllostomidae) is a migratory species that is distributed from central Mexico to the southwestern United States, occupying pine-oak and deciduous forest and desert scrub

(Arita 1991, Medellin 1994). Currently, this bat is listed as endangered by the United States (United States Fish and Wildlife Service 1988), Mexico (SEMARNAT 2010), and the International Union for the Conservation of Nature (Arroyo-Cabrales et al. 2008) due to declines in populations of over 50% in the past 10 years.

The Mexican long-nosed bat (*Leptonycteris nivalis*) is capable of moving pollen over long distances along its 1,200 km long migratory corridor. *L. nivalis* migrates every spring from central Mexico to the southern United States following the blooms of agaves (Moreno-Valdez et al. 2000). In the northern portion of this bat's range, agaves are their main food source (England 2012, Moreno-Valdez et al. 2004; EPGR & TEL unpublished data).

The migration of long-nosed bats is considered an "endangered phenomenon," due to the bats' particularities of roosting and foraging sites that they require (Arita and Santos-del-Prado 1999). Maintaining the agave corridor will allow *L. nivalis* to continue pollinating distant populations of agaves, thus enhancing their genetic diversity.

Conservation efforts for the endangered *L. nivalis* are hindered by the lack of information about the geographic distribution of the agave species that form the bat's "nectar corridor". In my first study (Chapter II), I modeled the potential geographic distribution of the nectar corridor using biodiversity informatics methods. Potential distribution has been referred to as the area estimated with presence only or presences/background data (Qiao et al. 2015). I used presence data of nine *Agave* species that I selected following three criteria: 1) paniculate *Agave* (genus *Agave* subgenus *Agave*) occurring within *L. nivalis* range, 2) reported in *L. nivalis* diet studies, 3)

documented to be flowering at the time *L. nivalis* is present in a particular area. I employed two presence-only distribution modeling techniques, in which I used statistical relationships between environmental data and known agave localities (Phillips et al. 2006, Stockwell and Peters 1999). I created a map of agave richness by overlapping the distribution maps of the 9 species. Then I determined if there is a spatial concordance between areas with higher number of *Agave* species and known *L. nivalis* localities. With this study I hope to provide managers with information that can help target areas for long-term monitoring and conservation efforts of the endangered bat and the agave corridor.

In the second study of my dissertation (Chapter III), I modeled the potential effects of climate change on the distribution of the bat *L. nivalis* and the same nine *Agave* species selected in Chapter II. I employed known species localities and bioclimatic variables (i.e. biologically meaningful variables derived from temperature and rainfall values) for current climate (representative of 1950-2000) and the most plausible low-end and high-end emission scenarios of four future climate models projected for 2050 and 2070. I analyzed the overlap between the distribution of the agaves and the pollinating bat in each future climate projection, and identified potential mismatches. These distribution changes could reduce the pollination service for the agaves and the available foraging resources for the endangered bat. These results could guide conservation efforts for maintaining the *Agave-L. nivalis* interaction over the long-term as a strategy to conserve the genetic variability and ecological resilience in agave

populations, and eventually mitigate effects of future climate change in arid and semi-arid ecosystems of Mexico and the United States.

In my third study (Chapter IV) I documented the impacts of three decades of land cover change in Mexico on the *Agave-L. nivalis* pollination corridor. I used land cover maps developed by Mexico's National Institute of Geography and Statistics (INEGI) for five time periods (1985, 1993, 2002, 2007, and 2011), and focused on changes that occurred in the three vegetation types where agaves are found (desert scrub, deciduous forest, and conifer forest). I created maps of available agave habitat for each time period by overlapping the maps of potential habitat for the selected 9 agave species (generated in Chapter II), and maps of the 3 targeted vegetation types in each time period. Then I calculated fragmentation metrics of the available agave habitat in each time period. Finally I estimated the percent of available agave habitat within the limits of protected areas in the most recent time period of the analysis (2011). With this study I aim to provide recommendations for managers to prioritize the restoration of agave populations.

Overall, by analyzing the potential effects of global and regional environmental changes on the *Agave-L. nivalis* corridor, this research can inform conservation practitioners to develop appropriate conservation efforts and help target priority areas and activities for the conservation of this endangered corridor.

# CHAPTER II

# MODELING THE POTENTIAL GEOGRAPHIC DISTRIBUTION OF AN ENDANGERED POLLINATION CORRIDOR IN MEXICO AND USA

## Synopsis

Endangered Mexican long-nosed bats (*Leptonycteris nivalis*) migrate up to 1,200 kilometers following the blooms of paniculate agave plants (genus *Agave*, subgenus *Agave*). My objective was to model the potential geographic distribution of this pollination corridor and to analyze if there is a spatial concordance between areas with higher number of *Agave* species and known *L. nivalis* occurrence. I selected nine *Agave* species based on the following criteria: 1) paniculate *Agave* (genus *Agave* subgenus *Agave*) occurring within *L. nivalis* range, 2) reported in *L. nivalis* diet studies, 3) documented to be flowering at the time *L. nivalis* is present in a particular area. I modeled the current distribution of those species using Maxent and GARP, and geographic information systems to analyze the spatial correspondence of *Agave* richness and presence of *L. nivalis*. For seven of the nine *Agave* species Maxent model performance outcompetes GARP. Maxent performance was higher particularly for species with small sample size ($\leq 7$). I combined the *Agave* presence maps to create a richness map showing up to five species overlapping. *L. nivalis* occurrence areas correspond with areas with two, three and four *Agave* species more often than random expectations at the 0.05 significance level. The opposite is observed for areas with cero *Agave* species where *L. nivalis* correspond less often than random. Presence-only

modeling tools allowed us to map potential agave presence. These maps could guide conservation actions to ensure the maintenance of this pollination corridor. Areas with higher number of *Agave* species are distributed along mountain chains and may provide foraging resources for bats for longer period of time during their migration. I recommend implementing a long-term monitoring program in those areas to document inflorescence timing in *Agave* species and the presence of *L. nivalis*.

## Introduction

Maintaining corridors that allow migratory pollinators to move between patches of plants is critical for preserving the genetic diversity of plant species and, as a result maintain the resilience of the ecosystem to changes in the environment. Animal pollinators like insects, birds and bats serve as mobile links among plant populations in different landscapes, facilitating pollen and gene flow over considerable distances. Plants have developed flowers with particular characteristics to facilitate their pollination. These flower traits are called pollination syndromes and reflect convergent adaptation for pollination by specific types of animals (Fenster et al. 2004).

Plants of the genus *Agave* (hereafter 'agaves') show chiropterophily, a flower syndrome with particular flower characteristics that attract bats (large and showy, white or light colored, open at night and with strong odors). Agaves are monocarpic, producing only one flower and ending their life cycle soon after. The age at which the plant produces the flower usually ranges between ten and 50 years. Agaves are considered keystone species in semiarid to arid regions, and their geographic center of origin is

Mexico. Their distribution is largely coincident with the distribution of nectarivorous bats. Studies suggest that the increase in speciation in agaves was precipitated by their colonization to arid environments and that particularly two species of bats specialized for nectar feeding (*Leptonycteris nivalis* and *L. yerbabuenae*) played an important part in this process (Good-Avila et al. 2006, Rocha et al. 2006).

Compared with other pollinators, bats are large-bodied and can carry larger pollen loads across distant populations of agaves (Fleming et al. 2009). Authors have suggested that the *Leptonycteris-Agave* interspecific relationship may be an example of coevolution and mutualism (Gentry 1982, Arita and Humphrey 1988, Arita and Martínez del Rio 1990). This relationship is clearer in agaves with a paniculate type of inflorescence (genus *Agave*, subgenus *Agave*), for which *Leptonycteris* has been reported to be not only relevant, but the single most important pollinator (Arizaga et al. 2000, Molina-Freaner and Eguiarte 2003).

*Leptonycteris* bats ensure cross-pollination in agave plants and, as a result, enhance agaves' genetic diversity and eventually increase the resilience of agave populations to environmental stress (Rocha et al. 2006). Agaves play a critical role in maintaining soil stability in deserts, xeric scrublands, and subtropical forests. Moreover, agaves have socio-economic value because historically they have provided food and cultural services for humans in the form of natural fibers and traditional beverages, such as tequila and mezcal (Gentry 1982, Colunga-García Marín et al. 2007).

The Mexican long-nosed bat (*Leptonycteris nivalis*, family Phyllostomidae) is a migratory species that is distributed from central Mexico to the southwestern United

States, occupying pine-oak and deciduous forest and desert scrub (Arita 1991, Medellin 1994). Currently, this bat is listed as endangered by the United States (United States Fish and Wildlife Service 1988), Mexico (SEMARNAT 2010), and the International Union for the Conservation of Nature (Arroyo-Cabrales et al. 2008) due to declines in populations of over 50% in the past ten years.

Evidence suggests that pregnant females of *L. nivalis* migrate up to 1,200 kilometers north from central Mexico to the southern United States every spring, following the blooms of paniculate agaves (Moreno-Valdez et al. 2000, Moreno-Valdez et al. 2004). The migration of long-nosed bats is considered an "endangered phenomenon", due to the bats' particularities of roosting and foraging sites that they require (Arita and Santos-del-Prado 1999). Conservation efforts for *L. nivalis* are hindered by the lack of information about the geographic distribution of the agave species that form the "nectar corridor" that this bat species follow during their migration.

In this study, I modeled a potential geographic distribution of this pollination corridor using biodiversity informatics methods. Potential distribution has been defined as the area estimated with presence only or presences/background data, using ecological niche modeling methods (Peterson and Soberon 2012, Qiao et al. 2015). In addition, I analyzed the spatial concordance of agave-rich areas with *L. nivalis* occurrence areas. My final goal was to provide insights for targeting areas for management and conservation of this endangered pollination corridor.

## Methods

### *Distribution modeling*

Peterson and Soberon (2012) point out the conceptual difference between ecological niche modeling (ENM) and species distribution modeling (SDM), asserting that genuine SDM must include steps of niche estimation and steps of assessment of dispersal ability or colonization potential. SDM requires presence and absence data of the species and to explicitly incorporate dispersal into analysis. These data is not often available and obtaining it requires field surveys that can be challenging and expensive to do in large and remote areas with complex topography. In such situations, one approach is to use presence-only data and limit area of analysis for each species to the ecological regions where they are found (Barve et al. 2011). The distributions obtained using presence-only data are referred to as "potential" (Qiao et al. 2015). Obtaining presence-absence data for the entire range of each species considered in this study would require time and resources investment that are not available, therefore, I created a potential distribution model for each species considered.

The "nectar corridor" followed by *L. nivalis* consists of *Agave* species that have flowering periods at different times of the year and the bat follows these blooming events during its migration (Moreno-Valdez et al. 2000). For modeling the potential geographic distribution of this corridor I selected *Agave* species according to the following criteria: 1) paniculate agave (genus *Agave* subgenus *Agave*) occurring within *L. nivalis* northern range, 2) reported in *L. nivalis* diet studies (Sanchez and Medellin 2007), 3) documented to be flowering at the time *L. nivalis* is present in a particular area

(Easterla 1972; Reid et al. 1985; Kuban 1989; Moreno-Valdez et al. 2004).

I condensed the total species found by searching for synonyms in the Plant List website (www.theplantlist.org). Finally, I obtained occurrence records for the agave species and for the bat *L. nivalis* from three on-line data repositories: the Global Biodiversity Information Facility (GBIF) data portal (www.gbif.org), the Comision Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), and the Mammal Networked Information System (MaNIS). In addition, I included records from literature (Baker 1956, Gentry 1982, Arita and Humphrey 1988, Hensley and Wilkins 1988, Jimenez-Guzman et al. 1999, Gonzalez-Alvarez 2005, Contreras-Balderas et al. 2007, Cabral-Cordero 2009), museum/herbarium collections (CIIDIR-IPN, FCB-UANL, UAAAN), and my field surveys. I eliminated records of cultivated agave specimens. The agave occurrence data were verified by specialists in agave taxonomy and ecology (Dr. Socorro Gonzalez-Elizondo and Dr. Martha Gonzalez-Elizondo from Instituto Politecnico Nacional).

Spatial autocorrelation in occurrence data creates spurious results and affects validation statistics. To lessen this effect, I rarefied the data and only considered occurrences situated at least 10 km apart based on the variation in topography and climatic conditions in the study region (Pearson et al. 2007, Wisz et al. 2008, Peterson et al. 2011). I considered only *Agave* species with at least five occurrence records after the rarefaction process. For species with 20 or more records, I subset randomly a group of points from each species' occurrence data to be used later for measuring performance of the model (model testing). The proportion of occurrences used for training each species'

model varied from 60 to 100 percent, depending on the total number of occurrences (Table 1).

Table 1. Proportion of occurrences used for training and testing each species' modeling exercise.

| Species | Number of records | Percentage for training | Percentage for Testing |
|---|---|---|---|
| *Agave palmeri* | 32 | 80 | 20 |
| *Agave havardiana* | 7 | 100 | 0 |
| *Agave inaequidens* | 25 | 80 | 20 |
| *Agave horrida* | 5 | 100 | 0 |
| *Agave salmiana* | 39 | 80 | 20 |
| *Agave parryi* | 43 | 80 | 20 |
| *Agave asperrima* | 92 | 60 | 40 |
| *Agave americana* | 38 | 80 | 20 |
| *Agave gentryi* | 24 | 80 | 20 |

The environmental variables used for building the models included three topographical variables: elevation, slope, and compound topographic index ("wetness index"), and 19 bioclimatic variables (Table 2). I downloaded the topographic layers from the United States Geological Survey's Hydro-1K data set (https://lta.cr.usgs.gov/HYDRO1K). I obtained the bioclimatic variables from the WorldClim database (www.worldclim.org) (Hijmans et al. 2005). All of the variables had a resolution of 0.0083°/px (ca. 1 $km^2$).

Table 2. Environmental parameters for species distribution models.

| CODE | VARIABLES |
|---|---|
| ELE | Elevation |
| SLO | Slope |
| CTI | Compound Topographic Index |
| BIO 1 | Annual Mean Temperature |
| BIO 2 | Mean Diurnal Range [Mean of monthly (max temp-min temp)] |
| BIO 3 | Isothermality ((BIO2/BIO7)*100) |
| BIO 4 | Temperature Seasonality (standard deviation * 100) |
| BIO 5 | Maximum Temperature of the Warmest Month |
| BIO 6 | Minimum Temperature of the Coldest Month |
| BIO 7 | Temperature Annual Range (BIO5-BIO6) |
| BIO 8 | Mean Temperature of Wettest Quarter |
| BIO 9 | Mean Temperature of Driest Quarter |
| BIO 10 | Mean Temperature of Warmest Quarter |
| BIO 11 | Mean Temperature of Coldest Quarter |
| BIO 12 | Annual Precipitation |
| BIO 13 | Precipitation of Wettest Month |
| BIO 14 | Precipitation of Driest Month |
| BIO 15 | Precipitation Seasonality (Coefficient of Variation) |
| BIO 16 | Precipitation of Wettest Quarter |
| BIO 17 | Precipitation of Driest Quarter |
| BIO 18 | Precipitation of Warmest Quarter |
| BIO 19 | Precipitation of Coldest Quarter |

Several studies highlight the importance of the geographic extent used during the modeling process due to effects on training (*e.g.,* size of training area results in different modeled suitable areas), validation (*e.g.,* larger extent makes the model look better than it actually is, when using the receiver operating characteristic (ROC AUC) as a validation method), and comparisons (*e.g.,* the niche similarity is affected by the extent or area of interest) (Lobo et al. 2008, Warren et al. 2008, VanDerWal et al. 2009, Anderson and Raza 2010, Jiménez-Valverde et al. 2011).

Barve et al. (2011) suggest considering only the area accessible for species dispersal and propose to use biotic regions. Biotic or ecological regions correspond to areas of general similarity in abiotic and biotic characteristics, and their boundaries can be informative about dispersal barriers, and can be considered a hypothesis of the areas that have been available to the species over relevant time periods. Therefore, for each species I delimited the extent of the environmental layers used for training the models, based on the Commission for Environmental Cooperation's ecological regions of North America Level II, which provide details useful for national and sub-continental overviews of physiography and wildlife (Commission for Environmental Cooperation 1997; www.cec.org).

Species distribution models estimate the relationship between species records at sites and the environmental and/or spatial characteristics of those sites (Franklin 2009, Elith et al. 2010, Miller 2010). There are many methods for modeling distributions but in regions where systematic biological survey data are sparse and/or limited in coverage, it is required to apply methods that work well with presence-only data. I used two modeling methods widely used when only presence data are available: maximum entropy (Maxent) (Phillips et al. 2006) and genetic algorithm for rule-set production (GARP) (Stockwell and Peters 1999). According to numerous studies both methods provide reasonable estimates of species' potential distribution (Elith et al. 2006, Peterson et al. 2011).

I applied the maximum entropy method using Maxent 3.3.2 software (Steven Phillips, AT&T Labs-Research, NJ, USA). This algorithm estimates the distribution

from a model of occurrence probability. I ran the models without duplicates to consider only one sample per pixel. I used the default conservative convergence threshold 1.0 x $10^{-5}$, and we set the test:training ratio depending on the total number of occurrences in the training subset for each species (Table 1). I ran ten replicate models for each agave species with different random set of background points and selected the best model based on the values closer to 1 of the receiver operating characteristic's area under the curve (ROC-AUC), which is a threshold independent evaluation of model performance.

To create presence maps of potential distribution I used the logistic output, a transformation of the raw probabilities that estimates the probability of suitable environmental conditions or probability of environmental conditions. I applied a threshold of occurrence for converting the continuous logistic output of Maxent to a binary prediction of "present" versus "absent". First, I defined a user-selected parameter *E*, which refers to the amount of error associated with the occurrence data. I set the *E* to 10% because most of the data came from collection databases and there is sampling bias associated with it. Then I obtained the suitability values of each occurrence point, and omitted 10% of points (*E* parameter) from the lower end of suitability (Lowest presence threshold – *E*), and used the next-highest suitability value as the cutoff for presence (above the cutoff = 1, below the cutoff = 0) (Pearson et al. 2007, Costa et al. 2010).

I used DesktopGarp 1.1.6 (R. Scachetti-Pereira, The University of Kansas Biodiversity Research Center) to run distribution models based on the GARP procedure. GARP searches iteratively for non-random correlations between species presence and environmental parameter values using several different types of rules. Each rule type

implements a different method for building species prediction models. I used the best subsets procedure (Anderson et al. 2003), running 100 models and selecting the best 10 models considering those under 10% of omission error and within 50% near the mean of commission error. I then summed these 10 best models grids to create a surface summarizing model agreement, with values ranging 0-10. The last step was to reclassify the 0 to 9 values as 0 and the value of 10 as 1 to obtain a presence (1)-absence (0) map. I used the software ArcGIS 10.2 (ESRI 2014) to perform this analysis.

*Evaluation of model performance*

A commonly used method to evaluate the distribution model predictions is the receiver operating characteristic (ROC) analysis, because it has the advantage of being threshold-independent. I used a modification of this approach, named the partial ROC (Peterson et al. 2008). The partial ROC approach allows comparing the performance of algorithms like Maxent and GARP that provide predictions across different spectrum of proportional areas in our study area.

I performed the partial ROC test using the computer program developed by Barve (2008). The program generates AUC ratios of the model AUC to the null expectation (random) through bootstrapping. I set up the program to select 50% of the total test points available with replacement 1000 times and considered a threshold of omission error (predicting absence when is presence) greater than 0.95, to consider only the portion of the ROC curve that lies within the range of acceptable models (omission error is more important in distinguishing good from bad models than commission error). Lastly, I assessed one-tailed significance of the differences in AUC from the line of null

expectations by using the z-statistic and calculating the probability that the mean AUC ratio is ≤1.

For species with fewer than 20 occurrences I evaluated model performance using a published jackknife approach (Pearson et al. 2007). I selected only the models that performed the best (higher success rate, and p-value <0.05).

*Concordance between predicted Agave richness and L. nivalis occurrence*

Using geographic information systems software (ArcGIS v. 10.2, ESRI 2014) I overlapped the final presence maps of each *Agave* species to produce a richness map. Then, I assessed the concordance between observed bat locations and agave richness using a Monte Carlo test (Manly 1997). Within a 50 km buffer around the 52 *L. nivalis* localities, I calculated the area with each possible value for agave richness. I then did this for buffer areas of 52 random points, and repeated it 1000 times to create a null distribution, to which I compared the data from the actual bat locations as a metric of significance. I considered 50 km for the radius of the buffer areas based on estimates of the bat's foraging range (Fleming et al. 2009; England 2012). I performed this analysis using Model Builder in ArcGIS (ESRI 2014).

**Results**

According to the criteria for selecting *Agave* species to be included in the model, the final list consisted of the following nine species: *A. americana, A. asperrima, A. gentryi, A. havardiana, A. parryi, A. salmiana, A. horrida, A. inaequidens, A. palmeri*. The distribution of the *Agave* occurrences is presented in Fig. 1.

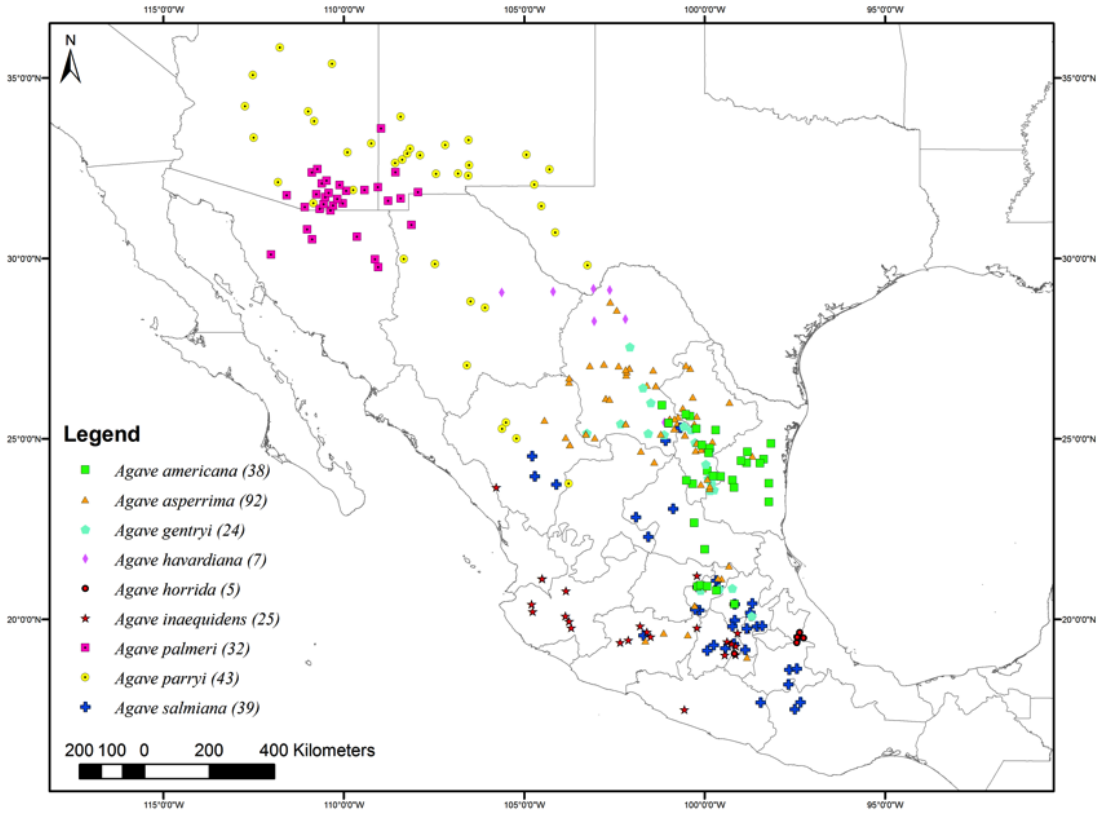



Fig. 1. Occurrences of selected *Agave* species. Total number of occurrence points is shown in parentheses.

I generated potential distribution maps of the *Agave* species using GARP and Maxent (Appendix A).

Model evaluation indicated that for seven of the nine agave species Maxent performed better than GARP (Tables 3 and 4). Maxent models of the two species with less than 20 occurrence records (*A. havardiana* and *A. horrida*) had higher success rate and significant p-values (<0.05) than the GARP models. GARP models performed better than Maxent for two species: *A. asperrima*, and *A. gentryi*.

Table 3. Results of the partial ROC test for evaluating model performance.

| Species | GARP | | | MAXENT | | |
|---|---|---|---|---|---|---|
| | Partial AUC* | p-value** | Number of replicates ≤1 | Partial AUC* | p-value** | Number of replicates ≤1 |
| *A. americana* | 1.44 | < 2.2e-16 | 0 | 1.67 | <2.2e-16 | 0 |
| *A. asperrima* | 1.18 | < 2.2e-16 | 0 | 1.14 | <2.2e-16 | 15 |
| *A. palmeri* | 1.81 | < 2.2e-16 | 0 | 1.86 | <2.2e-16 | 0 |
| *A. gentryi* | 1.88 | < 2.2e-16 | 0 | 1.78 | <2.2e-16 | 0 |
| *A. parryi* | 1.16 | < 2.2e-16 | 253 | 1.39 | <2.2e-16 | 0 |
| *A. inaequidens* | 1.11 | < 2.2e-16 | 364 | 1.56 | < 2.2e-16 | 0 |
| *A. salmiana* | 1.41 | < 2.2e-16 | 5 | 1.70 | < 2.2e-16 | 0 |

*Partial ROC value (Peterson et al. 2008, Barve 2008) – mean across 1000 bootstrap replicates
**Z-statistic

Table 4. Results of Jackknife evaluation of model performance for species with small numbers of occurrence records.

| Species | Locality sample size | GARP | | Maxent | |
|---|---|---|---|---|---|
| | | Success | p-value | Success | p-value |
| *A. havardiana* | 7 | 3 | 0.046395 | 6 | 0.026366 |
| *A. horrida* | 5 | 1 | 0.075852 | 2 | 0.000307 |

I produced a richness map combining the nine Agave *species* models (Fig. 2). The resulting *Agave* richness pattern appears to be associated with elevation finding suitable areas for more agave species in higher elevation areas (Fig. 3).

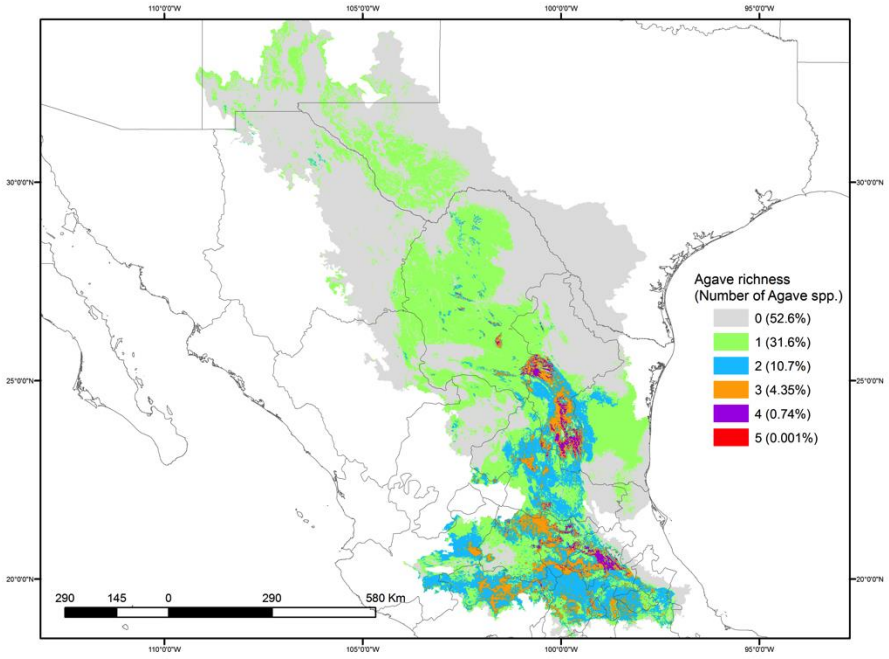



Fig. 2. Agave richness (number of *Agave* spp.). The percent of area per number of *Agave* spp. is shown in parentheses.

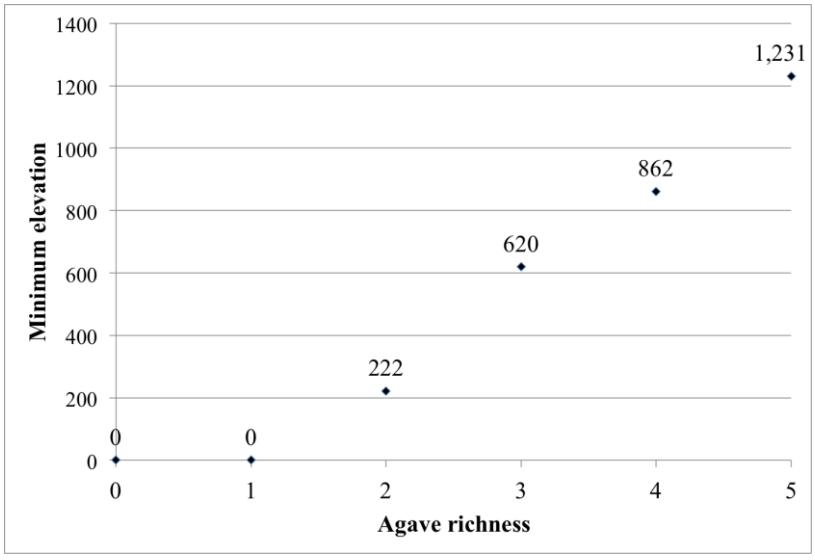



Fig. 3. Minimum elevation found within areas of each *Agave* spp. richness category.

The Monte Carlo simulation to assess the correspondence between observed bat locations and agave richness comparing to random expectations, shows that the 1000 random points replicates occurred more often in areas with zero agaves than the *L. nivalis* observed occurrences (Fig. 4, Table 5). The opposite was seen for areas with two, three and four agaves, where *L. nivalis* occurrences were more common than the random replicates. The results for areas with one and five agaves were not different from random at the 0.05 significance level (Table 5).

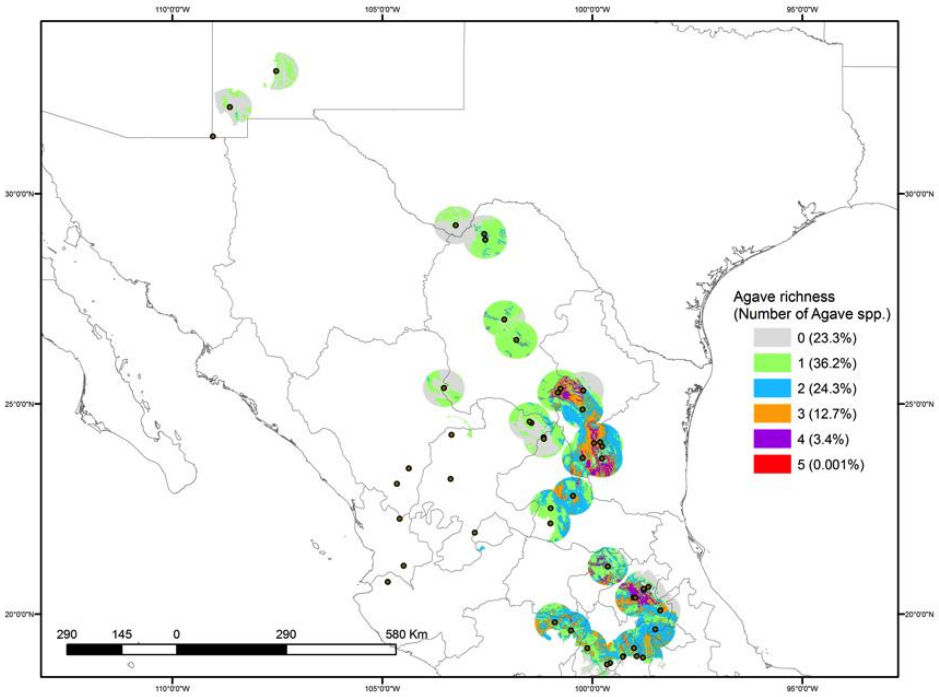



Fig. 4. Bat occurrence considering 50 km radius area and *Agave* spp. richness. The percent area per number of *Agave* species is shown in parenthesis.

Table 5. Monte Carlo test significance evaluation. The values represent the total number of pixels of each agave richness category. The observed values correspond to the area of occurrence of the bat *Leptonycteris nivalis*.

| | Agave richness (Number of *Agave* species) | | | | | |
|---|---|---|---|---|---|---|
| | 0 | 1 | 2 | 3 | 4 | 5 |
| Observed | 49102 | 76310 | 51313 | 26837 | 7134 | 2 |
| Mean Random | 99269 | 59512 | 20199 | 8350 | 1455 | 2 |
| $P_L$ | 0.002* | 0.894 | 1 | 1 | 1 | 0.768 |
| $P_U$ | 0.998 | 0.106 | 0* | 0* | 0* | 0.232 |

$P_L$ = Probability of a value as small or smaller than that observed
$P_U$ = Probability of a value as large or larger than that observed
* Indicates values < 0.05 level of significance

**Discussion**

My results are consistent with several publications that conclude that Maxent performs better than other algorithms when sample size is small (Hernandez et al. 2006, Pearson et al. 2007, Costa et al. 2010). For two of the nine agave species GARP outperformed Maxent, thus my results provide another example on the importance of considering more than one algorithm to obtain the best model for each particular species. Numerous papers compare the performance of different modeling algorithms, however it has been pointed out that it is almost impossible to establish all potential scenarios generating variation in the relative performance of the models, therefore the recommendation is to use several modeling algorithms (Terribile et al. 2010, Peterson et al. 2011, Qiao et al. 2015).

The models show that the *Agave* richness pattern appears to be associated with elevation. This finding would be expected considering that the elevation gradient in the mountainous regions results in more combinations of precipitation and temperature, and

suitable environments for a higher number of agave species.

The analysis of spatial correspondence between bat locations and areas with a higher number of agave species shows that the observed data co-occurs more frequently in areas with higher number of agave species and is different than random expectations. These findings make sense from two perspectives. First, considering that bats are efficient pollinators and have played a key role in the speciation of the genus *Agave* (Good-Avila et al. 2006), it would make sense to find a higher number of *Agave* species where *L. nivalis* is present. However, there are two other species of nectarivorous bats (*Leptonycteris yerbabuenae* and *Choeronycteris mexicana*) in some areas highlighted by the richness map, and their role as pollinators should be considered as well.

The second perspective considers the nectar availability for the bat. Areas with higher number of agave species would have nectar available through longer periods of time because the flowering season is different for each species (Gentry 1982), thus bats would prefer areas where they can find more foraging resources. During my fieldwork in the region I observed different species of agaves with flowers available at different times. Agave flowering varies latitudinally within species, however there is no published information available on the precise flowering timing at each location for each species considered in my study.

Some of the known occurrences for the bat did not overlap with any of the species of agaves considered in this study (Fig. 4). These occurrences are located in areas where the bat finds other plant species as foraging resources (*Stenocereus* spp., *Calliandra houstoniana*, *Bauhinia ungulate*, *Ceiba aesculifolia*, *Pseudobombax*

*ellipticum, Ipomoea arborescens*). Other *Agave* species present in central Mexico are not represented in the agave richness map because I focused on paniculate agaves with occurrences in northern Mexico and southern United States, where agaves are the only documented food source for *L. nivalis*. This has been confirmed for areas in Nuevo Leon and Coahuila by analyzing pollen found on the bats and identifying exclusively *Agave* pollen (EPGR and TEL unpublished data). The distribution of *L. nivalis* in the aforementioned region is restricted to available foraging areas (*Agave* populations) and roosting sites (*i.e.,* caves).

My models represent the potential distribution for each species, based on the environmental space information from the available occurrence data that might not be representing the entire niche for each *Agave* species, therefore it should not be assumed that the presence maps that I obtained are real distribution maps of the species. In spite of this, the methods I used have proven to be a good tool for identifying areas of species presence when there is a deficiency of field surveys. The large size, complexity of terrain and accessibility of our study area constrain the ability to conduct extensive field surveys to obtain presence and absence data necessary for creating more accurate distribution models. Presence-only modeling tools allowed me to obtain maps of potential presence needed for targeting areas for conservation actions to ensure the maintenance of this pollination corridor.

Nabhan (2004) describes the migratory corridors for winged pollinators as a mosaic of stepping-stones within a larger matrix, with each stone a stopover that migrants use for "refueling". This is the case for *L. nivalis – Agave* pollination corridor,

and it is fundamental to identify the geographic location of these "stepping-stones" to target conservation efforts. My results indicate that monitoring efforts should be targeted along the mountain chains in Nuevo Leon and Coahuila in Mexico, where bats potentially will find more foraging resources (*Agave* species) and roosting sites (caves). This is a region where biological surveys have been scarce particularly for bats and agaves.

In addition, further studies are necessary to confirm which agave species *L. nivalis* is foraging on and prioritize the maintenance of populations of those agave species. I recommend the implementation of a long-term annual monitoring program to obtain information on the phenology of *Agave* species. This information would help understand patterns and trends, such as mismatches in *Agave* flowering and presence of *L. nivalis*, and will allow creating informed decisions for mitigating negative effects on this endangered pollination corridor.

# CHAPTER III

# POTENTIAL EFFECTS OF CLIMATE CHANGE ON AN ENDANGERED POLLINATION CORRIDOR

## Synopsis

Modeling potential effects of climate change on the distribution of species helps guide management decisions for the conservation of endangered species. There is particular concern that such distribution shifts will affect biotic interactions, affecting critical ecological processes such as plant pollination. In this study, I modeled the potential distribution of an endangered migratory bat (*Leptonycteris nivalis*) and the group of plants they pollinate (*Agave* spp) during their annual migration from central Mexico to southern United States. I used two modeling algorithms, Maxent and GARP, to generate current distributions of environmentally suitable areas. I evaluated the performance of those models and selected the best algorithm to generate distributions under future scenarios. Maxent model evaluation outperformed GARP for seven of the nine Agave species, and GARP outperformed Maxent for the bat model. My models show that the suitable environments for all of the species would retreat to higher elevation areas, and the overlap between the *Agave* and the endangered pollinating bat will be reduced by at least 75%. Overall, my findings indicate potential negative effects of climate change on this pollination interaction. The reduction of suitable areas for *Agave* species will restrict the foraging resources available for the endangered bat, threatening the survival of its populations and the maintenance of their pollination service. The loss of key pollinators results in cascading effects at the ecosystem level.

The extinction of the bat *L. nivalis* will likely have a negative effect on the sexual reproduction and genetic variability of *Agave* plants increasing their vulnerability to future environmental changes. I recommend implementing a long-term annual monitoring program to document phenological mismatches in the *Agave- L. nivalis* interaction.

**Introduction**

Climate is one of the main variables determining the geographic distribution of a species (Grinnell 1917, MacArthur 1972). Studies have shown that, under future climate scenarios, the suitable areas for many species would change, reducing, increasing or shifting in latitude and elevation (Chen et al. 2011, Dullinger et al. 2012, Parmesan 2006, Root et al. 2003, Thomas 2010). There is concern that these distribution shifts will affect biotic interactions (Blois et al. 2013, Walther et al. 2002). Furthermore, there is evidence, that changes in climate are affecting plant phenology, delaying flowering periods and causing a mismatch with the presence of key migratory pollinators (Hegland et al. 2009, Tylianakis et al. 2008, Yang and Rudolf 2010).

Plants have evolved flower traits that reflect convergent adaptation for pollination by specific types of animals (Fenster et al. 2004). Plants of the genus *Agave* subgenus *Agave* (hereafter 'agaves') show particular flower characteristics that attract bats ('chiropterophily'). Studies on the reproductive ecology of agaves have shown that for several species the most effective pollinators are bats. Compared with other pollinators, bats are large-bodied and can carry greater pollen loads across distant

populations of agaves (Fleming et al. 2009).

Agaves play an important role in arid ecosystems, preventing soil erosion. According to biogeographic studies, Mexico is the center of origin of agaves (Good-Avila et al. 2006). The increase in speciation in agaves was precipitated by colonization of arid environments (Good-Avila et al. 2006). It has been hypothesized that two nectar feeding bat species (*Leptonycteris nivalis* and *L. yerbabuenae*) influenced the rapid speciation in agaves (Good-Avila et al. 2006, Rocha et al. 2006).

Authors have suggested that the *Leptonycteris-Agave* interspecific relationship may be an example of coevolution and mutualism (Arita and Humphrey 1988, Arita and Martínez del Rio 1990, Gentry 1982). Several studies have demonstrated that for several agave species, *Leptonycteris* bats are the most important pollinator (Arizaga et al. 2000, Molina-Freaner and Eguiarte 2003).

In this study I focus on the corridor of agaves used by the Mexican long-nosed bat (*Leptonycteris nivalis*). *L. nivalis* migrates up to 1200 km north from central Mexico to the southwestern United States every spring, following the blooms of paniculate agaves (Moreno-Valdez et al. 2000, Moreno-Valdez et al. 2004). This bat species is listed as endangered by the United States (United States Fish and Wildlife Service 1988), Mexico (SEMARNAT 2010), and the International Union for the Conservation of Nature (Arroyo-Cabrales et al. 2008) due to declines in populations of over 50% in the past ten years. Arita and Santos-del-Prado (1999) suggest conservation priorities for nectar-feeding bats and consider the migration of long-nosed bats an "endangered phenomenon" because of its complexity.

My research objective was to analyze potential effects of climate change in the geographic distribution of suitable areas for the bat *L. nivalis* and for key agaves forming its migratory corridor. I point out potential mismatches in the future distribution of agaves and the pollinating bat. These distribution changes could reduce the pollination service for the agaves, and the available foraging resources for the endangered bat.

## Methods

### *Study area*

The Mexican long-nosed bat (*L. nivalis*) is distributed from central Mexico to the southwestern United States, occurring in pine-oak and deciduous forest and desert scrub. Preliminary data that I have collected, in collaboration with the Palynology Lab from the Department of Anthropology at Texas A&M University, show that agaves are the only food source documented in the northern areas of the bat's distribution (EPGR & TEL unpublished data). Thus, I modeled only those agaves distributed in northern Mexico (Nuevo Leon and Coahuila) and the southwestern United States (Texas and New Mexico).

### *Species studied*

For modeling the potential geographic distribution of the corridor I selected *Agave* species according to the following criteria: 1) reported in *L. nivalis* diet studies (Sanchez and Medellin 2007); 2) documented to be flowering at the time *L. nivalis* is present in a particular area (Easterla 1972, Kuban 1989, Moreno-Valdez et al. 2004, Reid et al. 1985); 3) paniculate agave (genus *Agave* subgenus *Agave*) occurring within

the *L. nivalis* northern range.

I found a total of 30 names of agave species; however, many names were synonyms of the same species. To identify duplicated species I reviewed the Plant List website (www.theplantlist.org), which is a collaboration between the Royal Botanic Gardens, Kew and the Missouri Botanical Garden, and provides the accepted Latin name for most species, with links to all synonyms by which the species has been known.

The final list consisted of the following nine *Agave* species: *A. americana, A. asperrima, A. gentryi, A. havardiana, A. parryi, A. salmiana, A. horrida, A. inaequidens, A. palmeri*.

I obtained occurrence records for these agave species and for *Leptonycteris nivalis* from three online data repositories: the Global Biodiversity Information Facility (GBIF, www.gbif.org), the Comision Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), and the Mammal Networked Information System (MaNIS). In addition, I included records from literature (Arita and Humphrey 1988, Baker 1956, Cabral-Cordero 2009, Contreras-Balderas et al. 2007, Gentry 1982, Gonzalez-Alvarez 2005, Hensley and Wilkins 1988, Jimenez-Guzman et al. 1999), museum/herbarium collections (CIIDIR-IPN, FCB-UANL, UAAAN), and my field surveys. I eliminated records of cultivated agave specimens. All occurrence data from the above sources, were verified by experts in agave taxonomy and ecology (Dr. Socorro Gonzalez-Elizondo and Dr. Martha Gonzalez-Elizondo from Instituto Politecnico Nacional).

Spatial autocorrelation in occurrence data creates spurious results and weakens validation statistics. To lessen this effects I only considered occurrences situated at least

10 km apart (Pearson et al. 2007, Peterson et al. 2011, Wisz et al. 2008). I considered only *Agave* species with at least five occurrence records after the rarefaction process. For species with 20 or more records I subset randomly a group of points from each species' occurrence data to be used later for measuring performance of the model (model testing). The proportion of occurrences used for training each species' model varied from 60 to 100 percent, depending on the total number of occurrences (Table 1).

*Climate data*

For generating the potential future distributions of environmentally suitable areas for the species of interest, first I characterized the current (representative of 1950-2000) climatic niches using 19 bioclimatic variables obtained from WorldClim project (www.worldclim.com; Hijmans et al. 2005) with a resolution of 0.0083°/px (ca. 1 $km^2$). These variables are derived from temperature and precipitation data and represent annual trends, seasonality and extreme conditions.

The use of correlated and non-informative variables affects the degree to which the model can be spatially and temporally projected (Braunisch et al. 2013, Peterson et al. 2011). I selected appropriate variables following the steps used by Mendoza-González et al. (2013). First, I used Spearman correlation coefficients and eliminated those variables with the highest and most significant correlation coefficients ($r > 0.5$ and $P < 0.001$). The second step was to use Principal Component Analysis (PCA) to confirm the relative importance of the variables that were not correlated and thus explained the highest variance within the current climatic niche of each species based on the occurrence data.

I projected current distributions to 2050 (average for 2041–2060) and 2070 (average for 2061–2080) scenarios according to the Fifth Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (IPCC). The AR5 assessment uses Representative Concentration Pathways (RCPs) to address the uncertainty in climate projections due to future rates of greenhouse gas and aerosol emissions and levels of stratospheric ozone. RCPs refer to different levels of radiative forcing projected for the year 2100 (2.6, 4.5, 6, and 8.5 $W/m^2$). The radiative forcing is defined as the imbalance in longwave and solar radiation caused by changes in greenhouse gases and aerosols relative to preindustrial conditions.

A recent review paper entitled "Climate projections for ecologists" recommends that choosing a high and low emissions scenario is the best way of capturing the range of emissions' uncertainty (Harris et al. 2014). I selected two RCPs representing the most plausible low-end (RCP 4.5) and the extreme high-end (RCP 8.5) estimates. The increases in global mean temperatures projected for 2100 (relative to 1990) are 1.0-2.6°C for RCP4.5, and 2.6-4.8°C for RCP8.5.

I used Global Climate Models (GCMs, also referred to as General Circulation Models) from four different laboratories: Met Office Hadley Centre (HadGEM2-AO), Japan Agency for Marine-Earth Science and Technology (MIROC-ESM), NASA Goddard Institute for Space Studies (GISS-E2-R), and Centre National de Recherches Meteorologiques (CNRM-CM5). I selected the GCMs with the least deviation from the mean of all the models considered in a regional assessment for Mexico (Cavazos et al. 2013).

I downloaded the bioclimatic data for the ten different scenarios (4 GCMs X 2 RCPs X 2 time periods) from WorldClim project that contains downscaled IPCC-AR5 data at the same resolution as the current climate data (1 $km^2$). This resolution captures variability in topographic features in my study area, highlighting the difference between large valley bottoms and ridgetops, and allows a better prediction under climate change scenarios (Franklin et al. 2013a).

*Ecological niche modeling*

I used two ecological niche modeling algorithms, Maxent (Phillips et al. 2006) and GARP (Stockwell and Peters 1999), to characterize species' climatic niches for current conditions and project them to layers of selected potential future scenarios.

Maxent, maximum entropy modeling, estimates the ecological niche of species based on the location of maximum entropy distributions. I used the default Maxent program settings (version 3.3.3), except for the "extrapolation" and "clamping" options, which were disabled to avoid unrealistic extrapolations in the extreme values of the bioclimatic variables.

GARP, the genetic algorithm for rule-set production, searches iteratively for non-random correlations between species presence and environmental parameter values using several different rules. The algorithm selects rules mimicking a DNA evolution model (*e.g.*, deletion, mutation) for building species prediction models. I ran 100 models and selected the ten best models following the best subsets procedure (Anderson et al. 2003).

I compared the performance of the models produced with Maxent and GARP employing the partial AUC (Area Under the Curve) ratio (Peterson et al. 2008) with the

computer program for Partial ROC (Barve 2008), using the testing subset of points. I used the algorithm that performed the best for current conditions to model future distributions. For modeling future conditions I used all of the occurrence data points.

Finally, I created maps summarizing the changes between current and future potential distributions using the python-based SDMtoolbox (Brown 2014) in ArcGIS 10.2 (ESRI 2014). Also, I used ArcGIS 10.2 to create maps of overlapping areas between *L. nivalis* and all agaves; and maps of patterns of agave richness under current and future scenarios.

**Results**

According to the results of the correlation and PCA analysis, a different subset of bioclimatic variables was selected for modeling the distribution of suitable environments of each species (Table 6). The models show that the suitable environments for all of the species are reduced under future scenarios of climate change (Fig. 5). *Agave gentryi*, *A. horrida* and *A. salmiana* are reduced more than 80% under all scenarios, as well as *A. parryi* and *A. palmeri* under three scenarios (Table 7).

For *A. parryi*, *A. havardiana*, and *A. gentryi*, the GCMs ensemble for 2050 show greater loss of suitable area for the low-end RCP 4.5 than for the high-end RCP 8.5. The same trend is seen for *A. asperrima* and for the bat *L. nivalis* but in the two time projections 2050 and 2070. Overall the tendency in the RCP 8.5 scenario is towards aridity, and the localities of the five species that show less area loss under that scenario have the lowest annual precipitation values under the current conditions (Fig. 6).

The future models show a gain in suitable areas for six of the species in at least one of the RCPs and time frames. *A. palmeri* and *L. nivalis* show an increase in suitable areas in all of the scenarios. The highest gain is 5% for *A. palmeri* under RCP 4.5 and 2050 projection, and the gain for *L. nivalis* is 2% at the most (Table 7).

Table 6. Variables for each species modeling exercise. Variables selected after the PCA analysis are shown in bold. The units of variables marked with an asterisk are multiplied by 100.

| **Variables /*Species*** | *Agave americana* | *Agave asperrima* | *Agave gentryi* | *Agave havardiana* | *Agave horrida* |
|---|---|---|---|---|---|
| Annual mean temperature | **14.1-24.5** | **10.4-23** | **10.5-18.9** | **13.4-21.4** | **12-14.7** |
| Mean diurnal range | 11.1-17.8 | **12.5-19.3** | 13.6-17.3 | 12.9-16.3 | **13.9-15.62** |
| Isothermality* | **46-68** | 43-78 | 50-67 | **46-53** | **69-71** |
| Temperature seasonality* | **2069-5477** | **1028-6469** | 1653-5023 | **4654-6964** | **1621-1799** |
| Maximum temperature of the warmest month | **24.2-36.8** | **20.8-38.3** | 20.9-31.1 | **26-37.4** | **21.7-25.7** |
| Minimum temperature of the coldest month | **3-10.9** | 0-9.2 | 0-5.9 | **0-4.7** | **1.3-3.3** |
| Temperature annual range | **20.8-29.7** | 20.7-32.1 | **20.7-28.2** | 26-35.3 | **19.8-22.3** |
| Mean temperature of wettest quarter | 15.3-28.7 | **12.1-28** | **12.4-22.7** | 17.8-29.6 | **12.9-16.4** |
| Mean temperature of driest quarter | 11.2-22.5 | **9.4-18.8** | 7.6-15.5 | **10.5-13.9** | 9.6-12.1 |
| Mean temperature of warmest quarter | 16.6-29.2 | 12.7-30.7 | **13-23.5** | 18.7-29.6 | 13.9-16.6 |
| Mean temperature of coldest quarter | 11-18.6 | **7.4-17.2** | 7.2-14.6 | **6.8-12.3** | 9.6-12.1 |
| Annual precipitation | **323-976** | 199-1299 | **371-1037** | **258-484** | **406-1439** |
| Precipitation of wettest month | 57-245 | 39-317 | 66-227 | **41-93** | 86-321 |
| Precipitation of driest month | 4-16 | 3-24 | **4-22** | **3-10** | **5-12** |
| Precipitation seasonality (coefficient of variation) | **53-85** | **51-110** | **53-86** | **61-103** | **70-103** |
| Precipitation of wettest quarter | 155-503 | 93-752 | 166-553 | 117-266 | 195-906 |
| Precipitation of driest quarter | 22-69 | 15-80 | **18-78** | **12-39** | **17-38** |
| Precipitation of warmest quarter | **123-466** | 74-476 | **144-288** | **117-223** | **162-391** |
| Precipitation of coldest quarter | 22-84 | **23-86** | **30-82** | **15-50** | **20-45** |

Table 6 (Continued).

| **Variables /*Species*** | *Agave inaequidens* | *Agave palmeri* | *Agave parryi* | *Agave salmiana* | *Leptonycteris nivalis* |
|---|---|---|---|---|---|
| Annual mean temperature | **12-26** | 96-19.5 | 77-21.4 | **11.1-21.2** | 7.8-22.8 |
| Mean diurnal range | **12-17.3** | **12.8-20.7** | **15.3-20.6** | **13-17.8** | **12.7-19** |
| Isothermality* | 58-74 | 43-53 | 43-62 | 57-72 | 46-76 |
| Temperature seasonality* | **919-2959** | 5635-7486 | **3474-7770** | 1527-5018 | **1191-7381** |
| Maximum temperature of the warmest month | 22-34.6 | **27.7-37.7** | **25.3-41** | **20.8-34.9** | **17.9-34.9** |
| Minimum temperature of the coldest month | 0.6-17.7 | **-9.1-3.1** | **-11-2.8** | 0.7-9.1 | **-4.2-11.6** |
| Temperature annual range | 17-25.4 | 29.2-38.8 | 27.4-39.5 | 19.4-31 | 19.2-38.4 |
| Mean temperature of wettest quarter | 13-25.4 | 18.1-26.5 | **15.5-31.1** | 11.6-24.1 | 9.2-26.5 |
| Mean temperature of driest quarter | 9.5-26.1 | 12.6-21.5 | **7.7-24.9** | 9.1-18.6 | **6.7-22.8** |
| Mean temperature of warmest quarter | 13-27.2 | **18.6-27.3** | 16.1-31.5 | 13.1-25 | 9.9-27.4 |
| Mean temperature of coldest quarter | 9.1-24.8 | 1.2-11.8 | -1.1-11.8 | 8.9-18.6 | 4.9-20.2 |
| Annual precipitation | **816-1489** | 249-672 | 162-752 | 359-1264 | **240-1475** |
| Precipitation of wettest month | 157-372 | **58-148** | **28-192** | **65-256** | 45-360 |
| Precipitation of driest month | **2-11** | 3-13 | 2-12 | **1-18** | **2-28** |
| Precipitation seasonality (coefficient of variation) | 83-108 | **57-104** | 34-111 | **59-112** | **45-113** |
| Precipitation of wettest quarter | 440-944 | 145-327 | **63-480** | 166-708 | **106-870** |
| Precipitation of driest quarter | 17-60 | **12-48** | 10-53 | 12-58 | 11-99 |
| Precipitation of warmest quarter | **188-689** | **120-291** | 50-435 | 128-338 | **85-581** |
| Precipitation of coldest quarter | **25-201** | **44-180** | **22-173** | 12-73 | **14-153** |

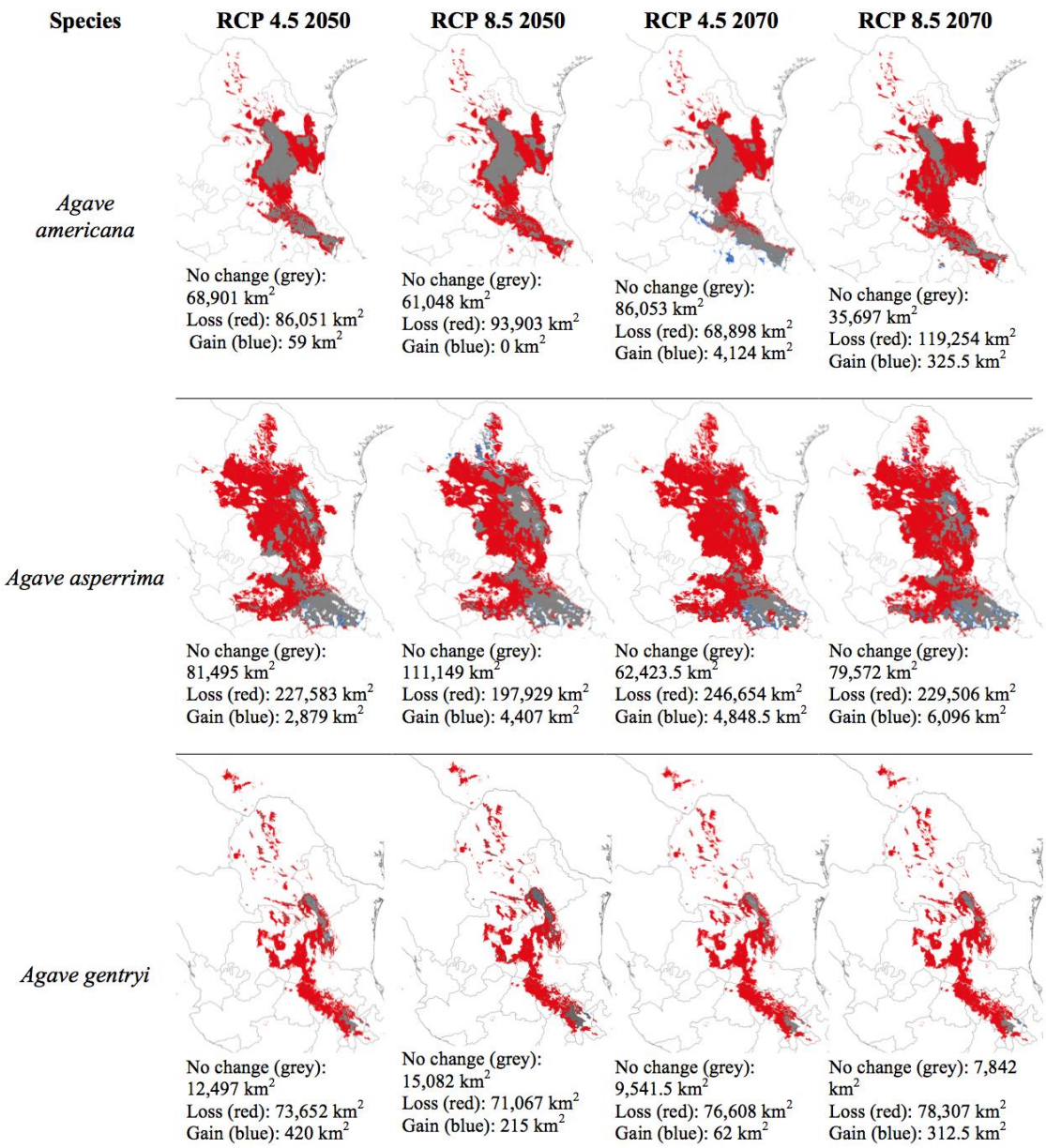



Fig. 5. Geographic distribution of gain and loss of suitable environments for all of the species under future scenarios of climate change.

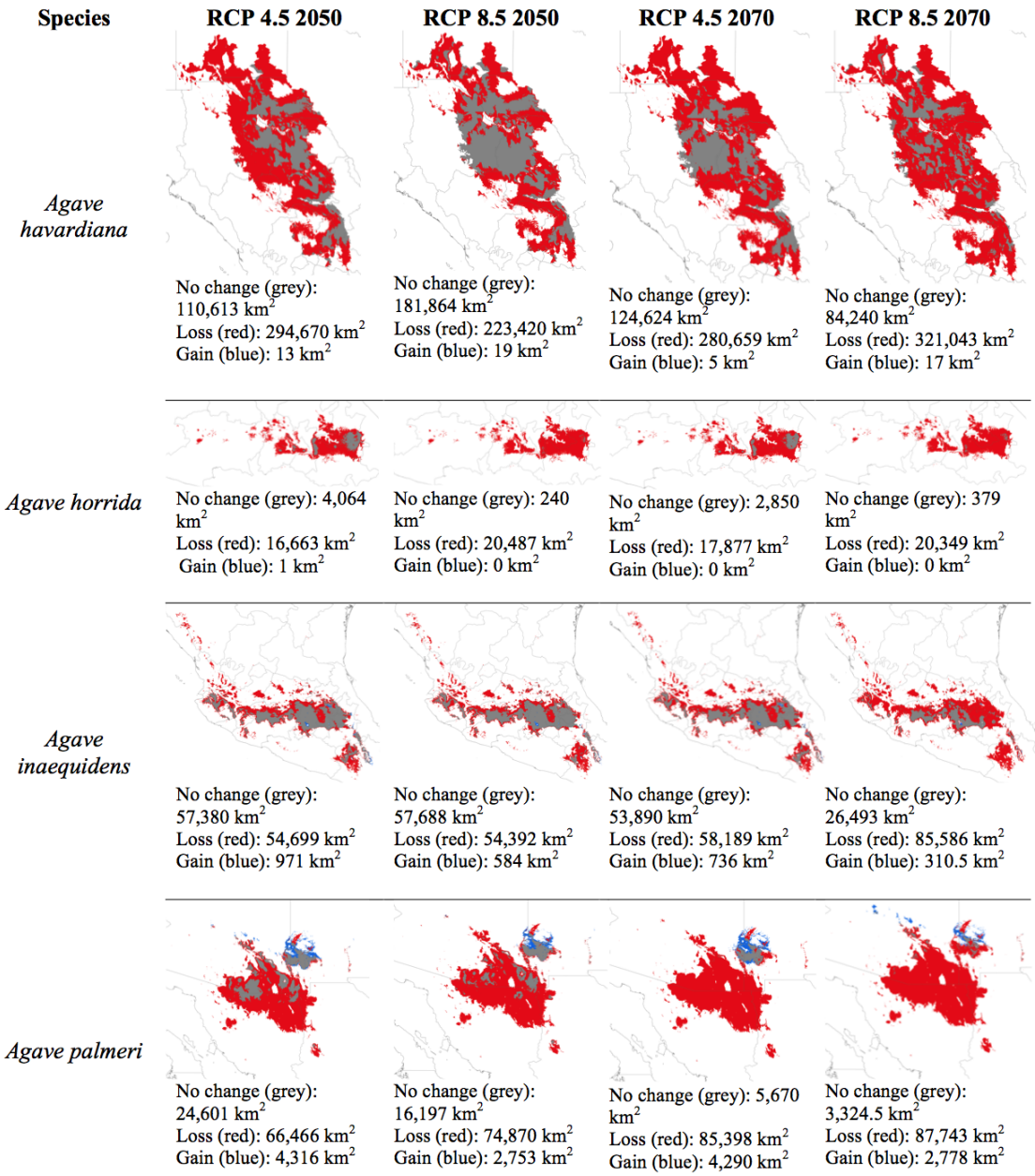



Fig. 5 (Continued).

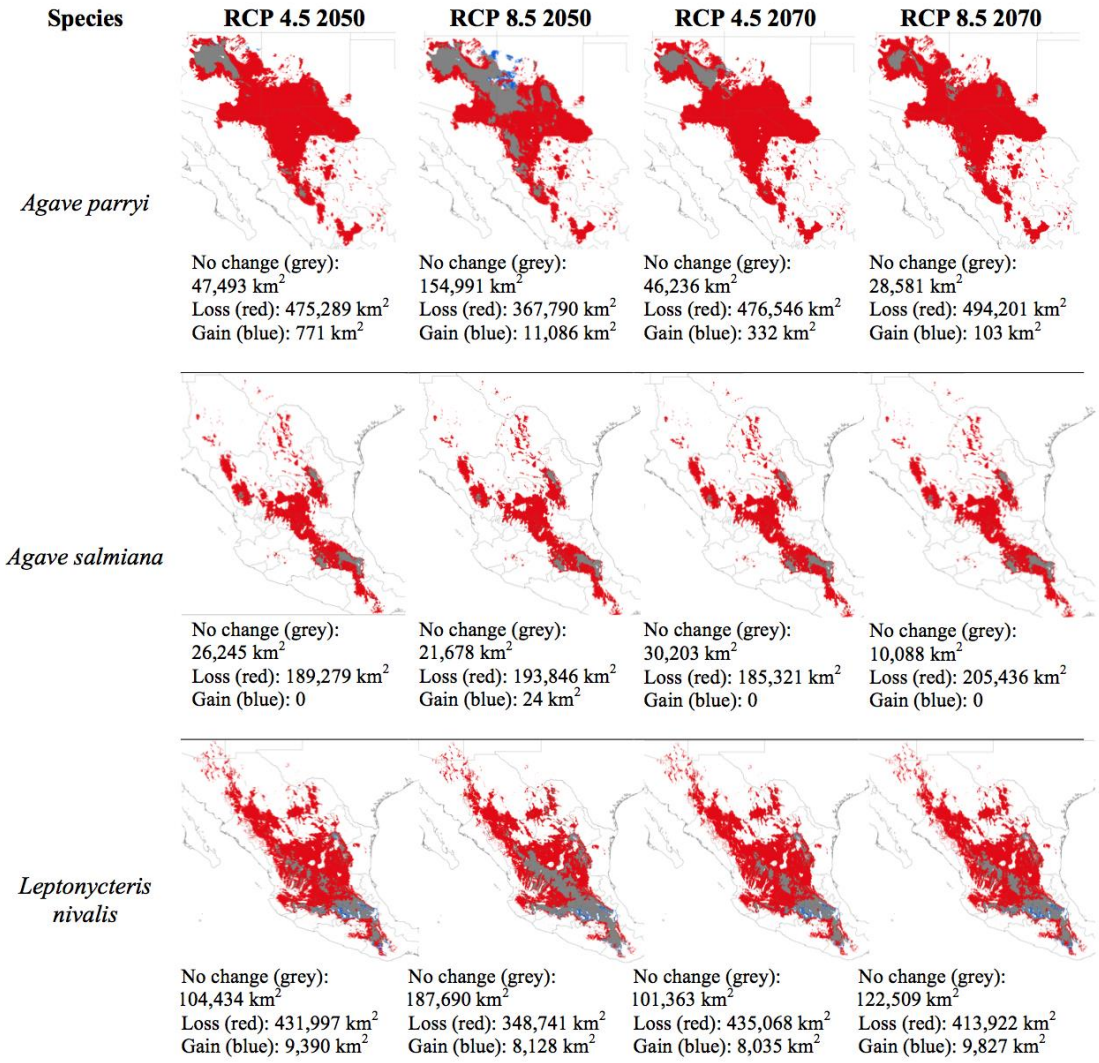



Fig. 5 (Continued).

Table 7. Percent of no change, loss and gain in each species' environmentally suitable area.

| Species | Scenario | No Change | Loss | Gain |
|---|---|---|---|---|
| *A. americana* | RCP 4.5 2050 | 44 | 56 | 0 |
| | RCP 8.5 2050 | 39 | 61 | 0 |
| | RCP 4.5 2070 | 54 | 43 | **3** |
| | RCP 8.5 2070 | 23 | 77 | 0 |
| *A. asperrima* | RCP 4.5 2050 | 26 | 73 | 1 |
| | RCP 8.5 2050 | 35 | 63 | 1 |
| | RCP 4.5 2070 | 20 | 79 | 2 |
| | RCP 8.5 2070 | 25 | 73 | 2 |
| *A. gentryi* | RCP 4.5 2050 | 14 | **85** | 0 |
| | RCP 8.5 2050 | 17 | **82** | 0 |
| | RCP 4.5 2070 | 11 | **89** | 0 |
| | RCP 8.5 2070 | 9 | **91** | 0 |
| *A. havardiana* | RCP 4.5 2050 | 27 | 73 | 0 |
| | RCP 8.5 2050 | 45 | 55 | 0 |
| | RCP 4.5 2070 | 31 | 69 | 0 |
| | RCP 8.5 2070 | 21 | 79 | 0 |
| *A. horrida* | RCP 4.5 2050 | 20 | **80** | 0 |
| | RCP 8.5 2050 | 1 | **99** | 0 |
| | RCP 4.5 2070 | 14 | **86** | 0 |
| | RCP 8.5 2070 | 2 | **98** | 0 |
| *A. inaequidens* | RCP 4.5 2050 | 51 | 48 | 1 |
| | RCP 8.5 2050 | 51 | 48 | 1 |
| | RCP 4.5 2070 | 48 | 52 | 1 |
| | RCP 8.5 2070 | 24 | 76 | 0 |
| *A. palmeri* | RCP 4.5 2050 | 26 | 70 | **5** |
| | RCP 8.5 2050 | 17 | **80** | **3** |
| | RCP 4.5 2070 | 6 | **90** | **4** |
| | RCP 8.5 2070 | 4 | **93** | **3** |
| *A. parryi* | RCP 4.5 2050 | 9 | **91** | 0 |
| | RCP 8.5 2050 | 29 | 69 | 2 |
| | RCP 4.5 2070 | 9 | **91** | 0 |
| | RCP 8.5 2070 | 5 | **95** | 0 |
| *A salmiana* | RCP 4.5 2050 | 12 | **88** | 0 |
| | RCP 8.5 2050 | 10 | **90** | 0 |
| | RCP 4.5 2070 | 14 | **86** | 0 |
| | RCP 8.5 2070 | 5 | **95** | 0 |
| *L. nivalis* | RCP 4.5 2050 | 19 | 79 | 2 |
| | RCP 8.5 2050 | 34 | 64 | 1 |
| | RCP 4.5 2070 | 19 | **80** | 1 |
| | RCP 8.5 2070 | 22 | 76 | 2 |

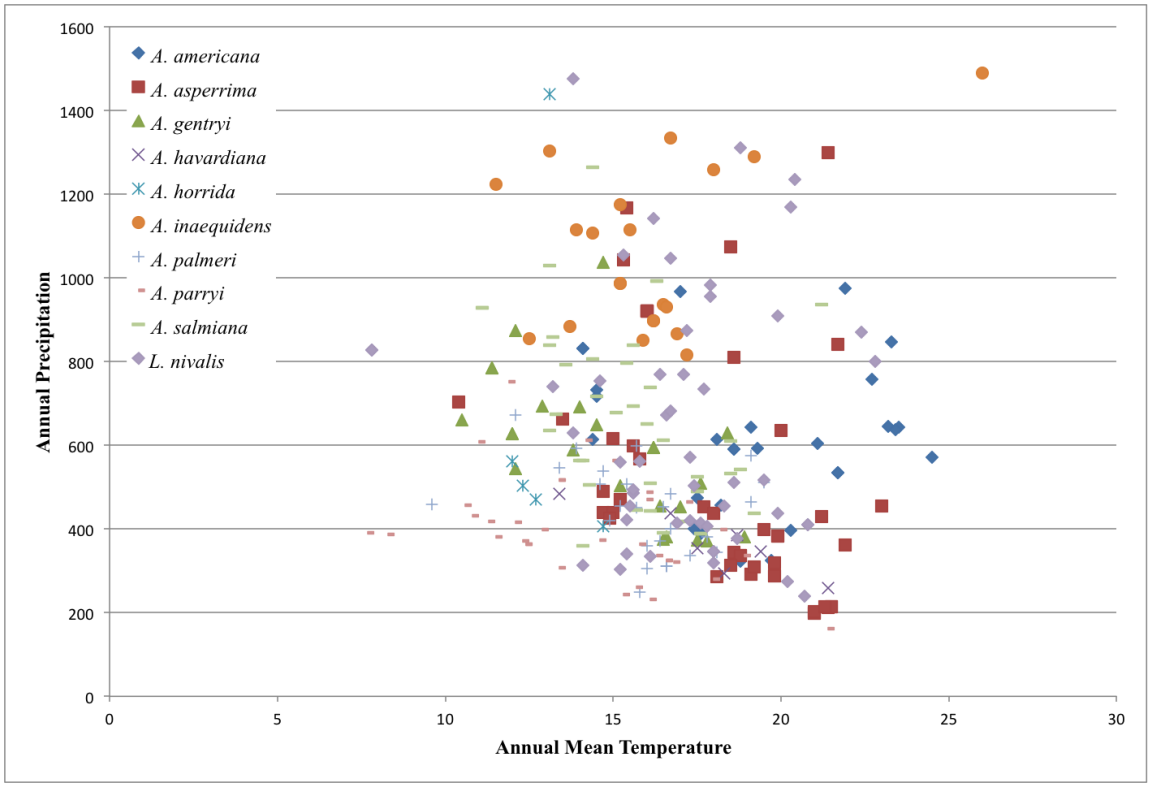


Fig. 6. Bidimensional ecological distribution (annual precipitation and mean temperature) of the species known occurrences.

The overall trend for all of the species is that the suitable areas would retreat to higher elevation areas in every future scenario considered in this study (Fig. 7).

I combined the presence area maps for each agave into one map representing the presence of one or more agaves. The overlap of this map with the suitable area map for the bat *L. nivalis* under current climatic conditions is 26.2%, and I found at least 75% decrease under all of the future scenarios (Fig. 8).

The results of Chapter II show a correspondence between areas with higher number of agaves and occurrence of the bat *L. nivalis*. Therefore I analyzed the change in the agave richness pattern under future climatic conditions (Fig. 9). The results show a

larger proportion of areas with cero agave species and a smaller proportion of areas with one or more agave in future scenarios than under current climate (Fig. 10).

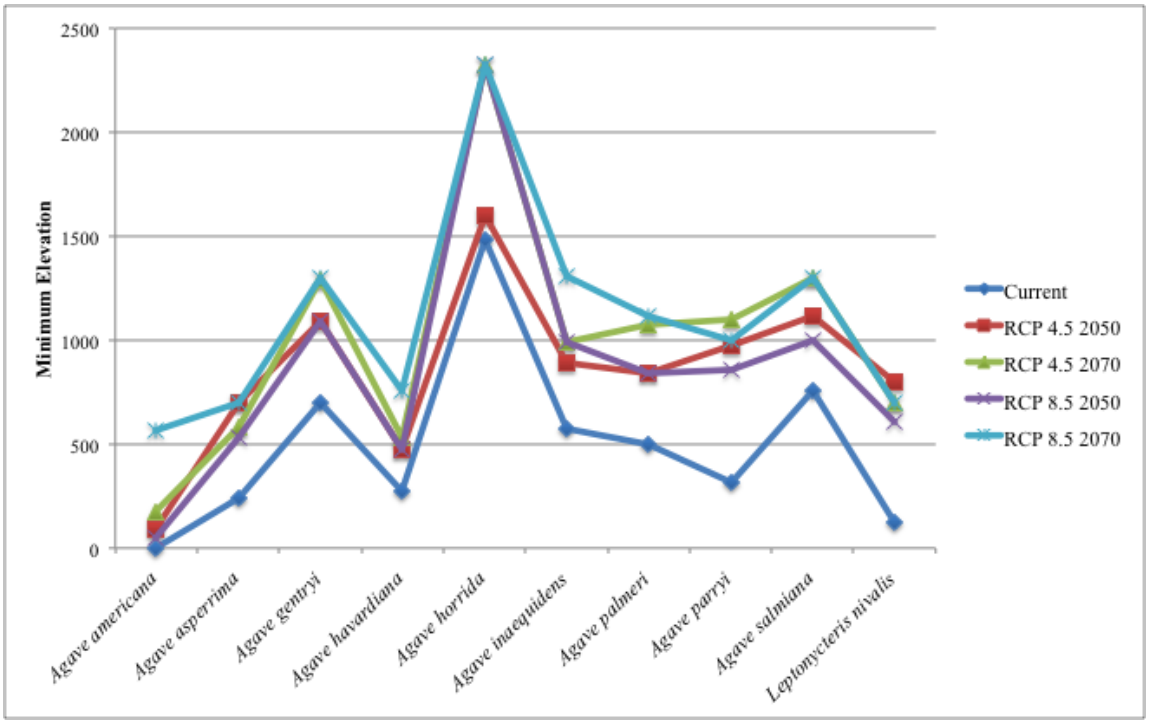
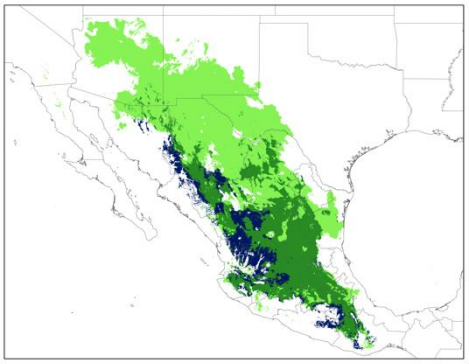


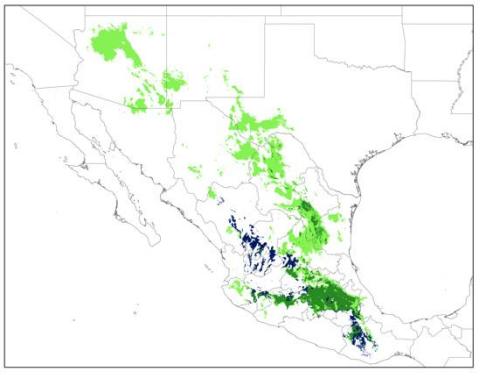
Fig. 7. Minimum elevation in the potential distribution areas of each species.

**Current**



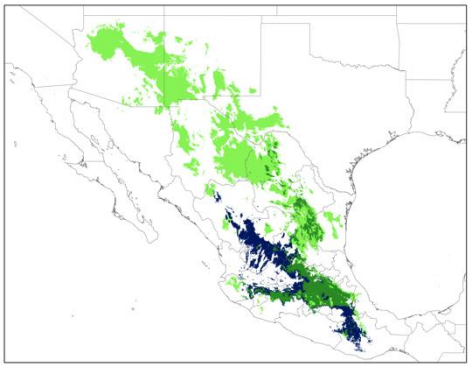
Percent overlap (dark green): 26.20%

**RCP 4.5 2050**



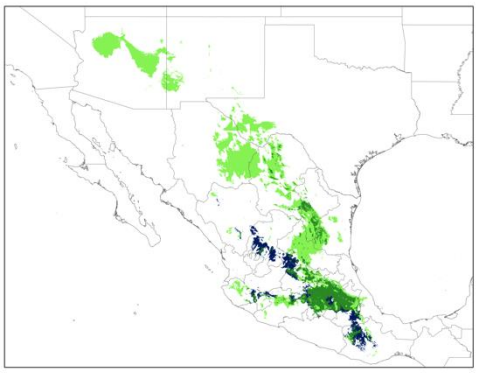
Percent overlap (dark green): 4.81 %

**RCP 8.5 2050**



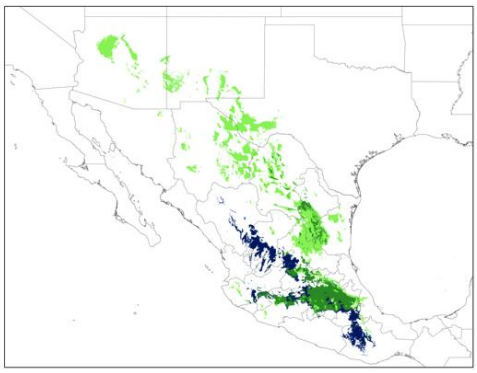
Percent overlap (dark green): 6.30 %

**RCP 4.5 2070**



Percent overlap (dark green): 4.51 %

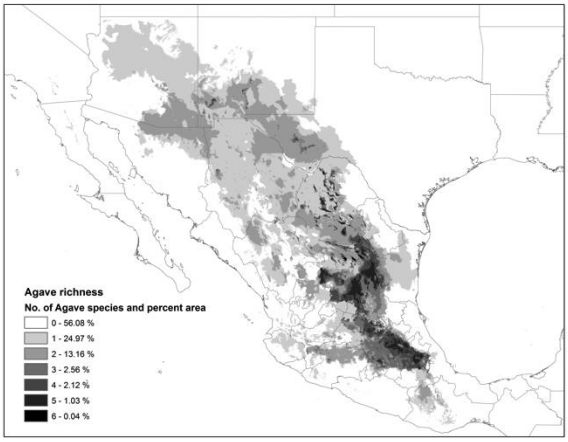
**RCP 8.5 2070**



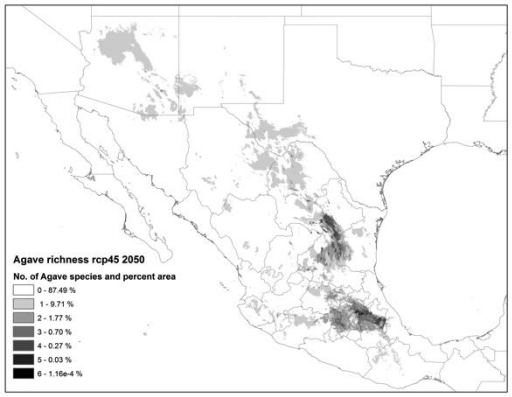
Percent overlap (dark green): 4.49 %

Fig. 8. Overlap (dark green) between environmentally suitable areas for *Agave* species (light green) and the bat *Leptonycteris nivalis* (blue).

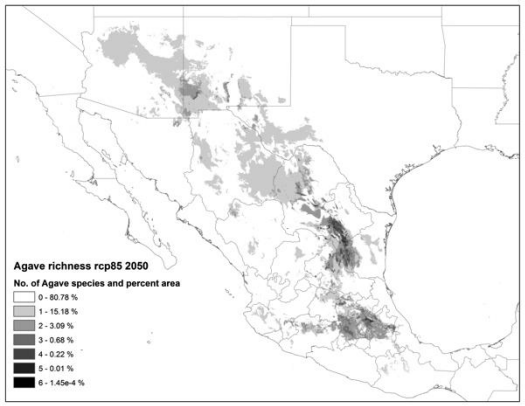
**Current**



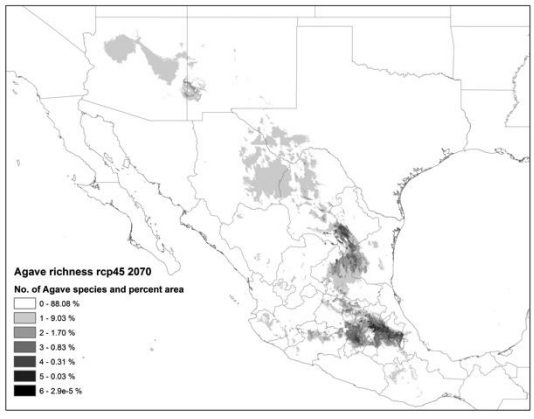

**RCP 4.5 2050**




**RCP 8.5 2050**




**RCP 4.5 2070**




**RCP 8.5 2070**

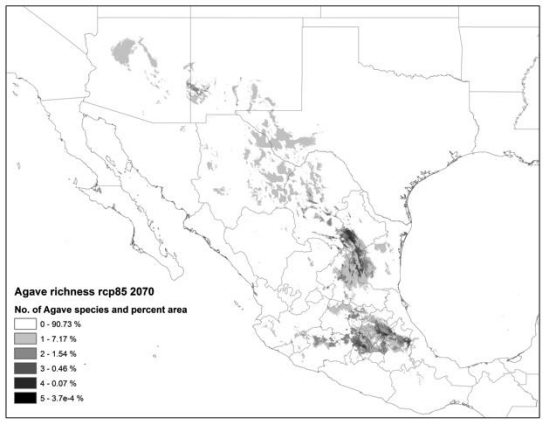



Fig. 9. Distribution of environmentally suitable areas for *Agave* species, under current and future climate scenarios.

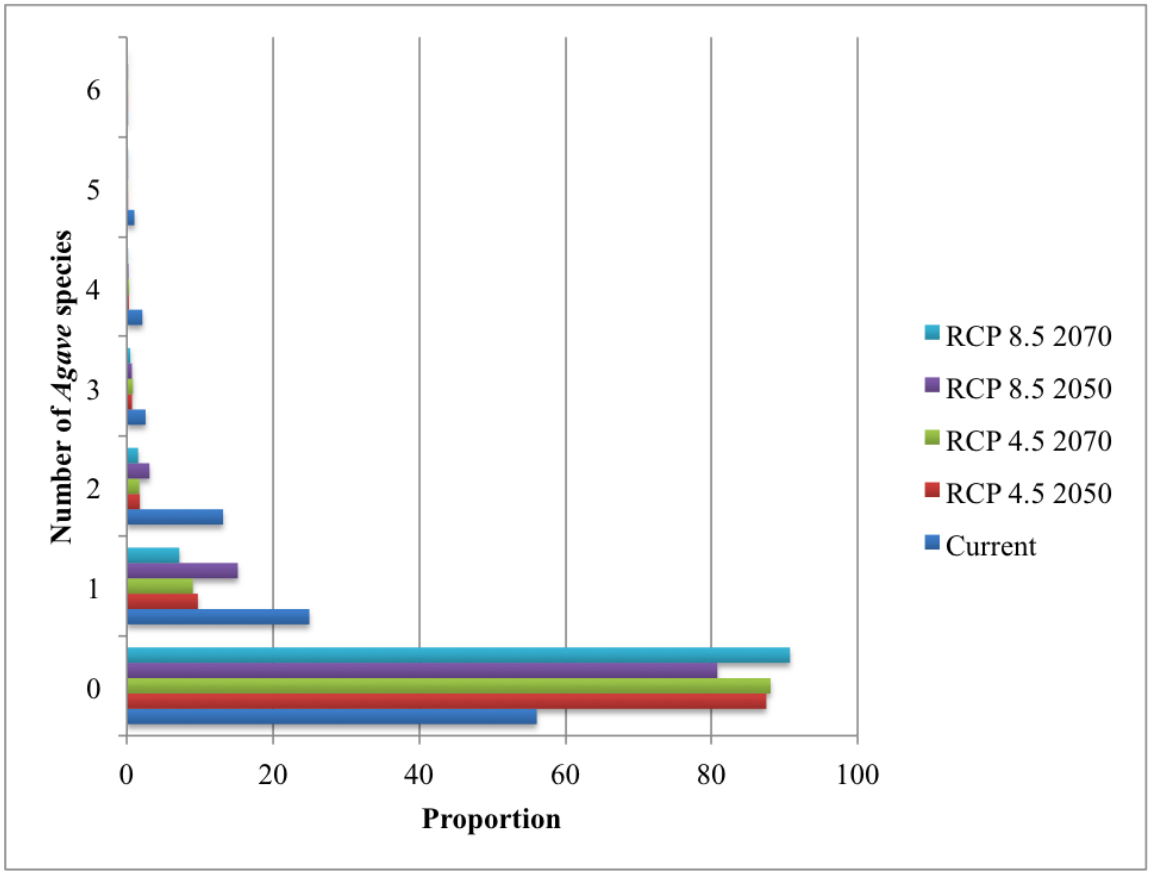



Fig. 10. Proportion of environmentally suitable area for different number of *Agave* species.

## Discussion

Previous studies analyzing the effects of future climate indicate a general trend for species retreating their ranges to higher elevation areas (Parmesan 2006, Parmesan and Yohe 2003). My results show the same trend for all of the species analyzed under all future scenarios. In general, it is expected that suitable environments for species will be reduced to a higher degree under the extreme high-end RCP 8.5. However, my results suggest that species that occur more often in areas with less precipitation, lose less area under the high-end RCP 8.5 than the low-end RCP 4.5.

There is current concern about the effects of climate change on the phenology of species and the resulting mismatches in biotic interactions (Blois et al. 2013, Miller-Rushing et al. 2010, Pau et al. 2011, Yang and Rudolf 2010). Of particular concern is the disruption in plant-pollinator interactions (Hegland et al. 2009, Kudo and Ida 2013, Memmott et al. 2007). My results suggest a reduction in the overlap of environmentally suitable areas for the agaves and the pollinating bat *L. nivalis.* The direction of this reduction is toward higher elevation areas along the Sierra Madre Oriental.

My models show that for some *Agave* species the overlap with *L. nivalis* completely disappears under future climate scenarios. Suitable areas for *A. parryi* and *A. palmeri* tend to retreat North, opposite to what the models show for *L. nivalis,* which tends to retreat South. Studies on the pollination biology of *A. palmeri,* suggest bats are important pollinators for this agave species (Hinman 2003, Scott 2004, Slauson 2000). Two other nectar-feeding bats (*L. yerbabuenae*, and *Choeronycteris mexicana*) occur within the range of *A. palmeri* and *A. parryi*. Nonetheless, *L. nivalis* would move pollen further distances because its migratory range is the largest of the three bat species.

Moving the pollen over long distances increases the opportunities for higher genetic diversity in the agaves, which expands the resilience potential of these plants to environmental change. In the long-term, the consequences of the mismatch between *L. nivalis* and agaves might result in the reduction or disappearance of agave populations. Wild agaves are important for maintaining soil stability and preventing erosion, and their absence would affect negatively the arid and semi-arid ecosystems where they occur.

I developed the models based only on bioclimatic variables, as a first

approximation to potential impacts of climate change on the distribution of species. Several reviews on modeling future species distributions recommend that in addition to climate, other variables should be considered. These variables include dispersal data, genetic adaptation, species behavioral plasticity, and biotic interactions (Anderson 2013, Blois et al. 2013, Schwartz 2012). Generating this information requires years of study and there is an urgent need to guide management actions for minimizing threats to biodiversity, even more in endangered systems like the *L. nivalis-Agave* interaction. My models are not predictions of future distributions but rather indicate the direction of change in the distribution of suitable environments for the *Agave* species and their pollinating bat *L. nivalis*. I did not find published references documenting the natural dispersal potential for the agaves considered in my study. Gentry (1982) mentions that, in general for all *Agave* species, most of the seeds produced, fall from the fruit capsules near the parent plant, but others in strong wind may be blown several meters. This suggests that agaves have a limited dispersal potential, and incorporating this variable in the models will likely restrict more the size of areas with suitable environments in future climate scenarios.

The presence of different species of agave along the bat migratory corridor allow for the availability of foraging resources for longer periods of time because each agave species flowers at a particular time frame (Gentry 1982). My models suggest that the pattern of agave richness dramatically changes in future scenarios, and the areas with two or more *Agave* species are greatly reduced. The fewer agave species present in one region reduces the period with available flowers. This might result in foraging stress for

the endangered *L. nivalis*, and force them to migrate to other areas earlier.

Changes in temperatures and precipitation will also affect the species phenology in ways we do not clearly understand. It is not clearly understood what the specific cues are, that trigger flowering in agaves, but there is consensus that precipitation is an important variable (Gentry 1982, Pau et al. 2011). I recommend implementing an annual monitoring program in the study area to document flowering timing in the agave populations and associated precipitation data. This information will help to understand long-term trends in the availability of foraging resources for the endangered bat *L. nivalis.*

Also, more research is needed on the reproductive ecology of agave species to better understand the role of *L. nivalis* in their pollination, and document which agaves are more dependent on the presence of the bat for their successful pollination and seed production. The loss of key pollinators results in cascading effects at the ecosystem level. The extinction of the bat *L. nivalis* will likely have a negative effect on the sexual reproduction and genetic variability of agaves, increasing their vulnerability to future environmental changes.

Agaves are an important food resource for several species of mammals, birds, and insects in arid ecosystems. Moreover, agaves help maintain soil stability and reduce erosion. Historically they have provided food and cultural services for humans, for example, natural fibers and beverages like tequila and mezcal (Gentry 1982). They are important in the regional economy, and carry strong social and cultural values.

Maintaining the *Agave-L. nivalis* interaction over the long-term would be a good

strategy for mitigating effects of future climate change in arid and semi-arid ecosystems of Mexico and the United States.

# CHAPTER IV

# IMPACTS OF LAND COVER CHANGE OVER THREE DECADES ON AN ENDANGERED POLLINATION CORRIDOR IN MEXICO

## Synopsis

One of the key drivers of pollinator declines is land cover change. I documented for the first time the impacts of three decades of land cover change in Mexico on an endangered pollination corridor. The animal pollinator in my study system is the nectar-feeding bat, *Leptonycteris nivalis*, considered endangered under national and international criteria due to over a 50% decline in their populations in ten years. This bat migrates every year following the blooms of *Agave* spp. from central Mexico to the southern United States; and is capable of moving pollen over its 1,200 km long migratory corridor, pollinating distant populations of *Agave* spp. Agaves have socio-economic value because historically they have provided food and cultural services for humans in the form of natural fibers, and traditional beverages such as tequila and mezcal. I used land cover maps developed by Mexico's National Institute of Geography and Statistics (INEGI) for five time periods: 1985, 1993, 2002, 2007, and 2011. I focused on changes that occurred in the three vegetation types where agaves are found (desert scrub, deciduous forest, conifer forest). I used the overlap of maps of potential agave habitat (created in Chapter II) and maps of the three targeted vegetation types in each land cover map, as the available agave habitat and calculated fragmentation metrics for each time period. My results indicate that a significant portion of desert scrub has

been lost mainly due to expansion in agriculture. The total number of patches has increased from 1985 to 2011, indicating fragmentation. Only 9% of the available agave habitat in 2011 was inside the limits of protected areas. I recommend restoring agave populations in depleted areas. This could help prevent soil erosion in the short term and provide multiple socio-economic benefits for the region, and, in the long term, could help maintain foraging resources for the endangered nectar-feeding bats.

## Introduction

Habitat loss as a result of human-induced land cover change is the most important factor contributing to biodiversity declines in Earth's terrestrial ecosystems (Millenium Ecosystem Assessment 2005). A rising concern is the decline in pollinators as a result of land cover change (Senapathi et al. 2015, Tscharntke et al. 2005, Winfree et al. 2011). Animal-mediated pollination contributes to the production of goods for humans. It also reinforces the reproduction of wild plants on which other services or service-providing organisms depend (Kremen et al. 2007).

The reproductive fitness of a plant depends substantially on the number of pollen grains transferred. An effective pollinator is able to transport the most pollen grains possible. Flowering plants have evolved particular flower characteristics that attract the most effective pollinators (Fenster et al. 2004). Flowers of plants of the genus *Agave*, subgenus *Agave* (hereafter agaves), are large and showy, white or light colored, have strong odors and produce more nectar during the night. These characteristics attract nectar-feeding bats, and for some agave species, bats are more efficient pollinators than

birds and insects (Arias-Coyotl et al. 2006, Arizaga et al. 2000, Molina-Freaner and Eguiarte 2003). Bats are large-bodied, compared with other pollinators, and can carry greater pollen loads across distant populations of agaves (Fleming et al. 2009).

Agaves are important plants in arid and semiarid ecosystems because they help to prevent soil degradation (Gonzalez Elizondo et al. 2009). In these ecosystems, food resources for nectar-feeding animals are scarce, and agave flowers are a key food source for several species of insects, birds and mammals. Moreover, agaves have economic and cultural value for humans, as they have been used for centuries in several cultures, for food, fiber, and the production of commercial products like mezcal and tequila (Gentry 1982, Colunga-Garcia Marin et al. 2007).

Among the nectar-feeding bats that pollinate agaves, the Mexican long-nosed bat (*Leptonycteris nivalis*) is capable of moving pollen over long distances along its 1,200 km long migratory corridor. *L. nivalis* migrates every spring from central Mexico to the southern United States following the blooms of agaves (Moreno-Valdez et al. 2000). In the northern portion of this bat's range, agaves are their primary food source (England 2012, Moreno-Valdez et al. 2004, EPGR & TEL unpublished data).

*L. nivalis* is considered endangered under national (US and Mexico) and international (International Union for the Conservation of Nature) criteria (Arroyo-Cabrales et al. 2008; SEMARNAT 2010; United States Fish and Wildlife Service 1988). Its populations have declined by more than 50% over the past ten years. Pregnant and lactating females have only been found in the northern range (Hensley and Wilkins 1988). Researchers have suggested that pregnant females give birth in northern Mexico

prior to their arrival in Emory cave at Big Bend National Park in Texas (Easterla 1972). Therefore, it is a conservation priority to maintain foraging resources in the northern range of *L. nivalis*.

In this study I used geographic information systems tools to analyze the effects of three decades of land cover change (LUCC) on the potential area of distribution of *Agave* species occurring in the northern Mexican portion of the bat's range. I identified fragmentation trends and suggest conservation opportunities to help maintain the endangered *L. nivalis – Agave* pollination corridor.

**Methods**

The study area encompassed the potential distribution of the *Agave* species that form the *L. nivalis-Agave* pollination corridor (created in Chapter II, Fig. 2). The northern portion of the corridor is where *L. nivalis* females give birth and where agaves are the main food source for the species. I focused this analysis on the northern portion of the corridor within Mexico (Fig. 11).

I used Land Use/Land Cover (LC) maps, scale 1:250 000, created by INEGI (Instituto Nacional de Estadistica y Geografia) using remote sensing imagery and field verification, and homologated for compatibility (details on Table 8). To date, INEGI has produced LC maps for the following time periods: 1985, 1993, 2002, 2007, and 2011. These maps are available for download from INEGI's website (www.inegi.org.mx) in vector format, and are the best available information on land use and land cover for Mexico at a regional scale. I used the software ArcGIS 10.2 (ESRI 2014) to convert the

LC maps to raster format with a pixel size of 100 m and reproject them to North America Albers Equal Area Conic. The vegetation classes that INEGI used in each LC map vary (Appendix B); therefore I reclassified into only nine classes of interest (Table 9).

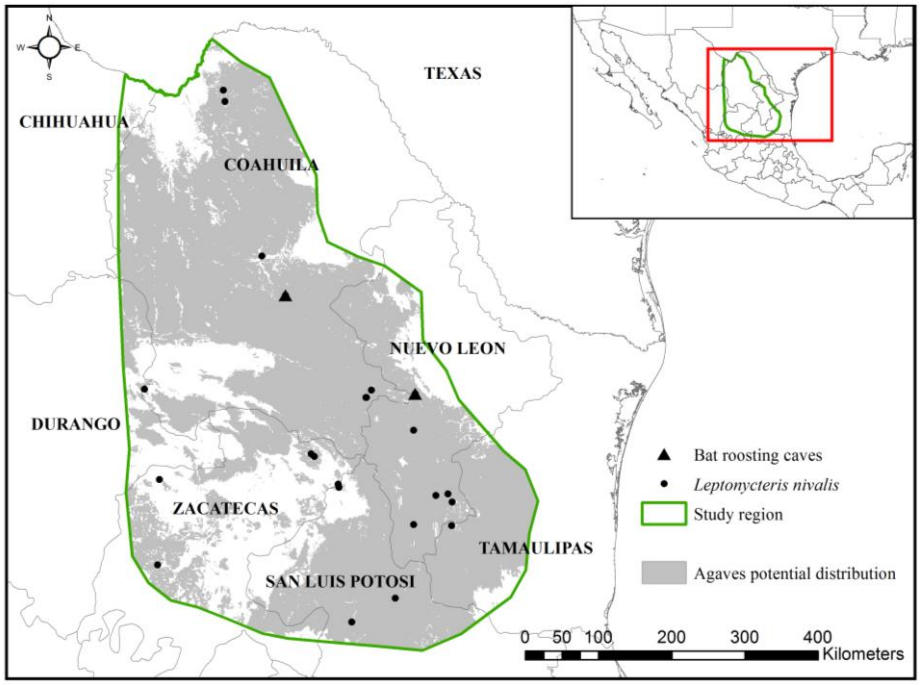



Fig. 11. Study region. The region was delimited considering the potential distribution of nine *Agave* spp. (Chapter II) and known occurrences of the bat *Leptonycteris nivalis*.

Table 8. Land Use and Land Cover maps, scale 1 : 250 000 (INEGI 2005, 2009, 2012, and 2014). Total number of land cover classes are different because some classes were broken down for some maps. For example, agriculture class was broken down into more categories in the earlier map series (Appendix B).

| Land cover map Series | Reference year | Total land cover classes in the study area | Elaboration |
|---|---|---|---|
| I | 1985 | 45 | Based on interpretation of aerial photographs taken between 1968 and 1986, and field verification |
| II | 1993 | 46 | Used Series I as a reference and incorporated Landsat TM composite imagery years 1993-1996, and field verification |
| III | 2002 | 43 | Used Series II as a reference and incorporated visual interpretation of Landsat ETM imagery, years 2002-2003, and field verification |
| IV | 2007 | 40 | Used Series III as a reference and incorporated visual interpretation of SPOT multispectral imagery, year 2007, and field verification |
| V | 2011 | 43 | Used Series IV as a reference and incorporated visual interpretation of LandSat TM5 multispectral imagery, year 2011 (dry season), and field verification |

Table 9. Description of the generalized land cover classes.

| Generalized land cover class | CODE | Description |
|---|---|---|
| Agriculture | AA | All types: seasonal, irrigation, cultivated grasslands, silviculture |
| Conifer forest | BC | Types: pine, pine-oak, and forest with *Pseudotsuga* sp. or *Picea* spp. |
| Deciduous forest | BD | Types: oak, oak-pine, and riparian forest with one or more of the following tree species: *Taxodium mucronatum*, *Salix* spp., *Fraxinus* spp., *Populus* spp., *Platanus* spp. and *Astianthus viminalis* |
| Water | H2O | Natural and man-managed water reservoirs |
| Other | NI | Vegetation types that are not *Agave* habitat |
| Bare ground | SV | Areas without vegetation naturally or due to anthropogenic influence |
| Desert scrub | VM | Succulent shrub, shrubs dominated by rosette plants (*Agave* spp, *Yucca* spp., *Dasylirion* spp.), creosote bush (*Larrea* spp.), shrub dominated by *Helietta parvifolia* and/or *Acacia berlandieri*. |
| Grassland | VP | All types of natural grasslands |
| Human settlements | ZU | Cities, Towns |

I used the Land Change Modeler software extension for ArcGIS (Eastman 2015) and the software ENVI 5.2 (ENVI 2010) to obtain land cover change statistics and transition matrices. In addition, I produced change maps of the vegetation classes where agaves occur: desert scrub, conifer and deciduous forest.

To identify fragmentation trends on the agave corridor, I created maps of available agave habitat for each time period. I did this by identifying the overlap of the potential agave habitat (obtained using ecological niche modeling tools in Chapter II), with the areas of the vegetation type where wild agaves occur. Other studies have used

ecological niche models to evaluate the impacts of land cover change on species (López-Arévalo et al. 2011; Peterson et al. 2006; Rios-Muñoz and Navarro-Sigüenza 2009; Sanchez-Cordero et al. 2005; Yañez-Arenas et al. 2012). First, I extracted from the LC maps the areas of the three vegetation classes where wild agaves occur (desert scrub, deciduous forest, conifer forest), and created a binary raster where the value of 1 indicated presence of the targeted vegetation classes. Next, I used the potential distribution maps of agaves created in previous analysis (Chapter II) and combined them into one binary raster where 1 indicated presence of at least one agave species, and 0 indicated absence of all species. Then I summed the binary raster obtained from the LC map and the binary raster obtained from the agave distribution models. I reclassified the output raster to create a binary raster where 1 indicated available agave habitat. This raster had a pixel resolution of 1 km. Finally, using the raster of available agave habitat, I calculated landscape metrics commonly used as indicators of fragmentation: total number of patches, mean patch size, and mean nearest neighbor distance. These metrics were obtained using Patch Analyst extension for ArcGIS (Rempel et al. 2012).

Additionally, I estimated the amount of remaining agave habitat in the latest land cover map (2011) that is located within protected areas designated by Mexico's national commission on protected areas (CONANP). In this study, I focused only on human-driven land-use changes and did not include other factors, such as climate change, that could affect the distribution of agaves.

## Results

Agaves in the study region are found in three vegetation classes: desert scrub, deciduous forest, and conifer forest. Desert scrub had the largest cover area in all five LC maps used (Fig. 12, Table 10). The land cover change analysis indicates that desert scrub was the class with the largest negative net change from 1985 to 2011, and most of this change occurred between 1985 and 2002 (Fig. 13). The average annual net loss in desert scrub area has decresed from the early time intervals (1985-1993) to the latest (2007-2011) (Table 11). The analysis of contributions to the net change in desert scrub shows that most of the area transitioned to agriculture (Fig. 14).

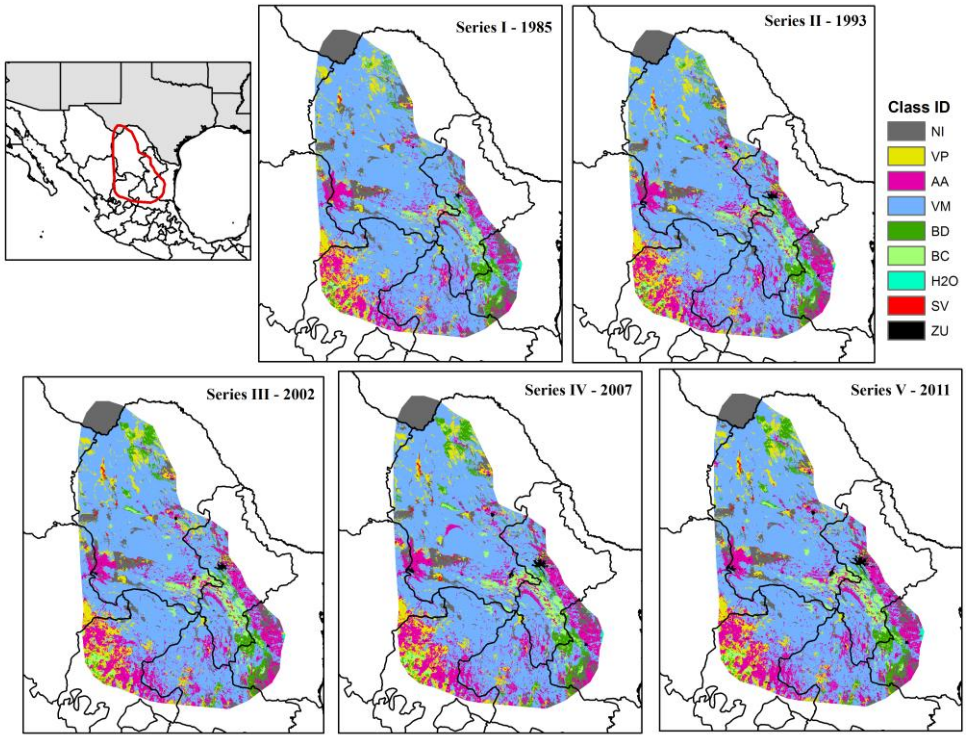



Fig. 12. Land cover maps and classes for the study area. AA=Agriculture, BC=Conifer forest, BD=Deciduous forest, H2O=Water, NI=Other, SV=Bare ground, VM=Desert scrub, VP=Grassland, ZU=Human settlements.

Table 10. Total area ($km^2$) for each land cover class in the different LUCC maps. AA=Agriculture, BC=Conifer forest, BD=Deciduous forest, H2O=Water, NI=Other, SV=Bare ground, VM=Desert scrub, VP=Grassland, ZU=Human settlements

| Generalized Land Cover Class | Series I 1985 | Series II 1993 | Series III 2002 | Series IV 2007 | Series V 2011 | Total difference between 1985 and 2011 |
|---|---|---|---|---|---|---|
| AA | 32,188 | 37,979 | 39,932 | 41,449 | 42,054 | 9,866 |
| BC | 7,614 | 8,276 | 10,320 | 10,487 | 10,367 | 2,753 |
| BD | 7,983 | 8,388 | 11,650 | 11,835 | 11,720 | 3,737 |
| H2O | 289 | 464 | 449 | 485 | 643 | 354 |
| NI | 28,323 | 26,371 | 24,688 | 24,230 | 25,007 | -3,316 |
| SV | 648.58 | 714.48 | 750.84 | 904.83 | 861.81 | 213 |
| VM | 182,648 | 176,002 | 169,982 | 170,073 | 168,826 | -13,822 |
| VP | 22,858 | 23,313 | 23,721 | 21,457 | 21,172 | -1,686 |
| ZU | 214 | 1,299 | 1,310 | 1,882 | 2,155 | 1,941 |

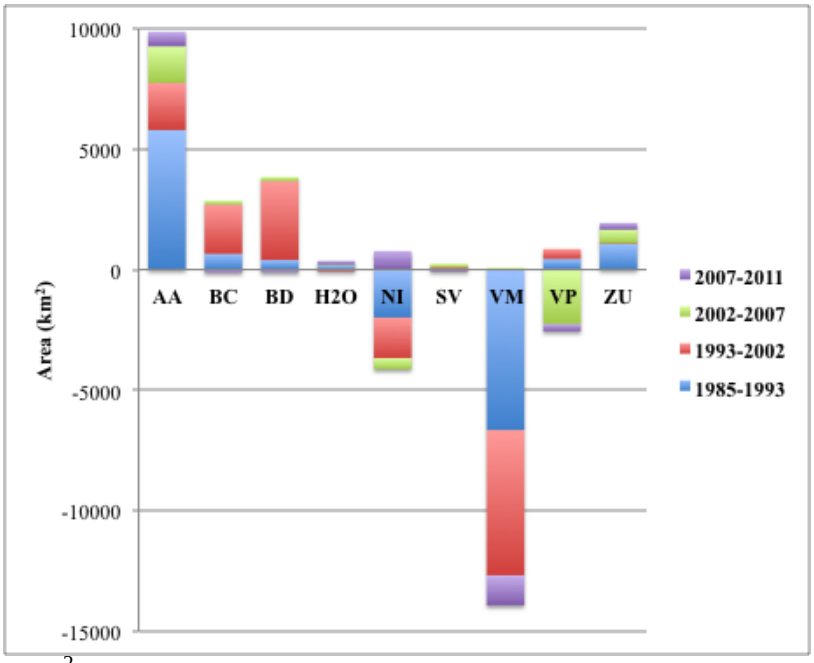



Fig. 13. Area ($km^2$) net change (original area + gain – loss) per land cover class. AA=Agriculture, BC=Conifer forest, BD=Deciduous forest, H2O=Water, NI=Other, SV=Bare ground, VM=Desert scrub, VP=Grassland, ZU=Human settlements

Table 11. Average annual net change in area ($km^2$). Positive numbers indicate a gain, negative numbers indicate a loss. AA=Agriculture, BC=Conifer Forest, BD=Deciduous Forest, VM=Desert scrub

| | Class | | | |
|---|---|---|---|---|
| Image Intervals | AA | BC | BD | VM |
| 1985-1993 (8 years) | 724 | 83 | 51 | -832 |
| 1993-2002 (9 years) | 217 | 227 | 363 | -669 |
| 2002-2007 (5 years) | 303 | 33 | 37 | 18 |
| 2007-2011 (4 years) | 151 | -30 | -29 | -312 |

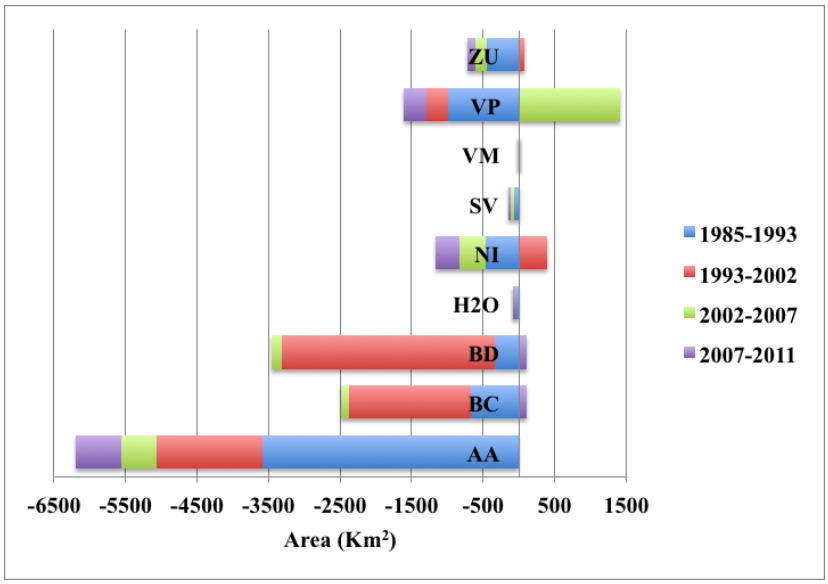



Fig. 14. Contributions to net change in desert scrub. The horizontal axis indicates the area ($km^2$) either gained (positive) or lost (negative) and to which class the area transformed. AA=Agriculture, BC=Conifer forest, BD=Deciduous forest, H2O=Water, NI=Other, SV=Bare ground, VM=Desert scrub, VP=Grassland, ZU=Human settlements

The desert scrub area loss between 1985 and 1993 occurred in areas located in the central eastern portion of Coahuila adjacent to Nuevo Leon; and the area loss between 1993 and 2002 occurred in areas located in the northern portion Coahuila within the study area (Appendix C).

My analysis indicates that conifer forest and deciduous forest increased mainly between 1993 and 2002 (Fig. 13, Table 11). Deciduous forest increased primarily in the northeastern portion of the state of Coahuila, within the study area (Appendix C); and the increase in conifer forest is largely observed in the sierras between the state of Coahuila and Nuevo Leon (Appendix C). Desert scrub contributed the most to the increment in the two types of forest (Appendix D).

I calculated percent change for each class. Percent change is the area for a class divided by the area of a class in the later cover image and multiplied by 100. The class with the highest value of percent change was human settlements with 84% area increase between 1985 and 1993 (Appendix E).

The maps of available agave habitat for each time period show a reduction of 2% from 1985 to 2011(Fig. 15), and 9% of the remaining agave habitat in 2011 is within the boundaries of protected areas designated by Mexico's commission on protected areas (CONANP) (Appendix F). The landscape metrics calculated indicate an increase in the number of habitat patches after 1985. The largest mean patch size was observed in 1985. The mean nearest neighbor distance between patches remained similar in all the time periods analyzed (Table 12).

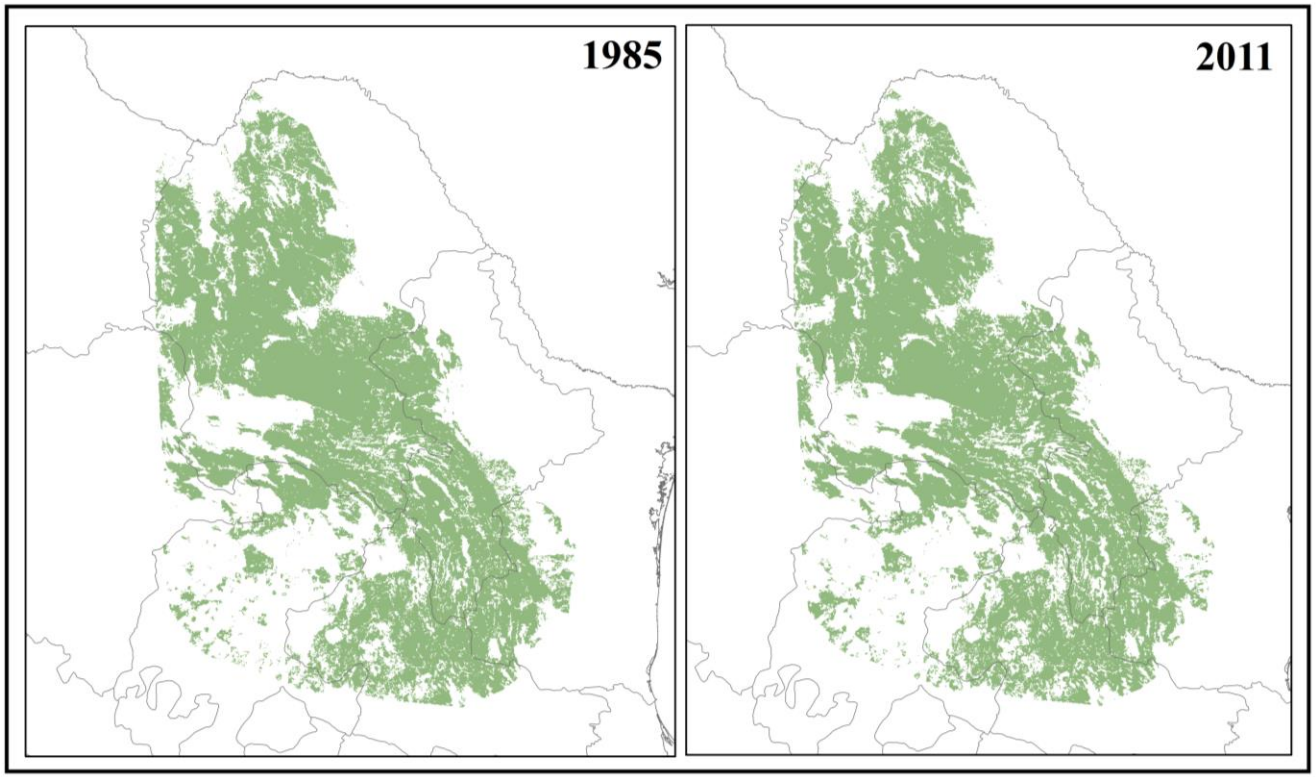


Fig. 15. Agave habitat available in 1985 and 2011.

Table 12. Landscape metrics for each land cover map.

| Land cover map | Number of patches | Mean Patch Size ($km^2$) | Proportion of Landscape Area | Mean nearest neighbor distance (km) |
|---|---|---|---|---|
| I (1985) | 711 | 21.52 | 77.22 | 1.55 |
| II (1993) | 783 | 19.04 | 77.42 | 1.54 |
| III (2002) | 780 | 19.11 | 77.70 | 1.54 |
| IV (2007) | 760 | 19.73 | 77.99 | 1.53 |
| V (2011) | 740 | 20.15 | 78.14 | 1.54 |

**Discussion**

I centered my analysis on the changes in the three vegetation types where agaves occur in the study region: desert scrub, deciduous forest, and conifer forest.

My findings on the degradation of desert scrub are consistent with other LUCC studies for Mexico (Perez Miranda et al. 2012, Trucios Caciano et al. 2012). Desert scrub is the most common vegetation type in Mexico, occupying 29% of the territory. By 2011 10% (5.8 million hectares) of the desert scrub area was transformed. The main cause of this transformation is the expansion of agricultural areas (SEMARNAT 2013).

Within my study area, the LUCC analysis indicates that most of the loss in desert scrub between 1985 and 1993 occurred in the central eastern portion of Coahuila adjacent to Nuevo Leon, probably due to the expansion of the main urban areas in the region (Monterrey, Saltillo and Monclova) along with agricultural activities around the cities.

The results indicate an increase in deciduous and conifer forest replacing areas previously occupied by desert scrub. This finding is expected considering the possibility of natural forest succession over the time lapse of my analysis. In the desert scrub

category I included scrublands, which are found adjacent to forest in the foothills of mountains and it is possible that forest extended into those areas. Other land cover change studies in Mexico report similar trends, showing an increase in forest areas (Moreno-Talamantes and Garcia Aranda 2012, Trucios Caciano et al. 2012). The gain in deciduous forest between 1993 and 2002 in areas located in northern Coahuila could have been the result of the implementation of conservation activities in the area after the creation of the federal protected area Maderas del Carmen in 1994 (CONANP 2008).

The increase in human settlements after 1985 in the region was likely the result of migration of people seeking employment opportunities with the growing industries (*e.g.*, mining, energy, manufacturing, construction) in the main cities of the region: Monterrey, Saltillo and Monclova. Since the 1970s, Mexico has seen an urbanization trend, with approximately 77% of the total population currently living in cities. The abandonment of rural areas reduces the local pressure on the land use, and has been related to natural vegetation recovery in several countries, including Mexico (Bonilla-Moheno et al. 2012). The abandonment of rural areas in the study region could have contributed to the small increase in desert scrub and forest areas.

Agriculture and cattle ranching are the main driving forces of the degradation of ecosystems in arid regions, such as our study region (Arriaga 2009; Challenger 1998). Still, there are other human activities that are threatening this region, such as mining. Mining has been an important economic activity since the early 1900s, and significant portions of the landscape have been directly and indirectly affected by this activity, by degradation of the vegetation and pollution of the soil (Challenger 1998). Mining

activities are not included in the land cover maps created by INEGI, but would add interesting and important information as another major regional land use threat.

The increase in number of available agave habitat patches over the time intervals studied, suggests a fragmentation trend. Habitat degradation is still the most important contributor to habitat loss and subsequent fragmentation. As mentioned earlier, there are impacts of mining activities in the landscape and in the soils that are likely contributing to fragmentation in agave habitat. More recently, the growing development of wind farms and plans for shale gas extraction in the region are potentially additional fragmentation forces.

Moreover, significant portions of the region have been affected by severe drought and fire. Between 1998 and 2013, the state of Coahuila had the largest proportion of area affected by fires in the country, with more than 580 000 hectares burned (SEMARNAT 2015). Most of this area is located within my study area. During my field surveys in 2012 and 2013, I observed the effects of the severe drought that occurred in 2011 affecting large areas in northern Mexico. The drought affected extensive cattle ranching activities because there was not enough forage available for the cattle and, as an alternative, the cows foraged on any vegetation available, including agaves, increasing the level of degradation.

The recovery of depleted vegetation in arid lands is slow. For instance agaves are slow-growing plants that bloom only at the end of their life cycle at 10 - 50 years. The migration of the endangered *L. nivalis* relies on the agave blooming events. In order to have blooming agave every year, there needs to be agaves in late life stages. Even if

depleted areas are restored with agaves, there will be a time lag for blooming events to occur meaning that restoration needs to happen as soon as possible to account for this lag. The fragmentation and disturbance on the available agave habitat can result in the lack of mature agave to produce flowers, and this would disrupt *L. nivalis* migration. Climate change is another factor that would affect the distribution of agave habitat, however for this study I focused on direct human-driven land-use changes.

An additional threat to the migratory *L. nivalis* in the study region is the development of wind farms. Currently, wind turbines are operating in Nuevo Leon and Tamaulipas, in areas that are within the potential distribution of the migratory corridor. A report by the Woodrow Wilson International Center for Scholars and United States Agency for International Development (USAID) highlights areas with potential for wind energy generation in Tamaulipas, Nuevo Leon, and Coahuila, within the corridor (Wood et al. 2012). Large numbers of bats are killed at wind energy facilities in North America (Baerwald et al. 2014, Cryan et al. 2014). However, researchers are proposing strategies to help mitigate the negative effects of wind energy on bats (*e.g.*, avoid placing wind farms in migration routes, turn off turbines with low wind because there is higher bat activity). These strategies should be considered in current and future wind farms facilities operating in the study region, along with on-going monitoring of bat activity, particularly during the spring and summer months when the endangered *L. nivalis* migrates to the region.

Overall, my results highlight the need for the implementation of conservation strategies to mitigate fragmentation and degradation in the *Agave-L. nivalis* corridor. The

pressures on the land cover change are a result of actions performed by various actors (government, private sector, local communities). Conservation strategies should be developed with participation of all of the actors. Recent efforts to engage local actors for the protection of bats and their habitat in our study region have demonstrated the value of engaging regional NGOs and local communities (Gomez-Ruiz et al. 2015).

I recommend implementing restoration activities of agave populations in depleted areas. This would prevent soil erosion in the short term, and would provide foraging resources for the endangered nectar–feeding bats in the long term, and maintain the *Agave-L. nivalis* pollination corridor.

# CHAPTER V

# CONCLUSIONS

In this dissertation I sought to contribute to the understanding of consequences of global and regional environmental changes on the endangered *L. nivalis-Agave* corridor. The tight synchrony between the timing of *L. nivalis* migration and the peak nectar availability of flowering *Agave* along the corridor can easily be disrupted by climate change or by human-induced land cover change.

Conservation efforts for the *L. nivalis-Agave* corridor are hindered by the lack of information about its geographic location. In the first study of this dissertation (Chapter II), I developed a potential distribution model of paniculate *Agave* species that make this corridor using two ecological niche modeling algorithms: GARP and Maxent. These two algorithms allow developing potential distribution models with presence-only data. Their performance varies depending on the species, but it is not clear what characteristics of the species data would allow one to perform better than the other. As part of the analysis in Chapter II, I compared the performance of both algorithms, and concluded that Maxent outperformed GARP in most of the species analyzed, however there were two species where GARP performed better. My findings support literature recommendations on using several algorithms for modeling species distributions instead of relying on one.

Also in Chapter II, my results indicate that bats occur more often in areas with higher number of *Agave* species and is different than random expectations. This finding is evidence of the mutualistic interaction between *L. nivalis* and agaves. The presence of

several species of agaves within the foraging range of the bat, allows for nectar availability for longer time period. Also, since the bat is transporting pollen and contributing to the genetic variability in agaves, then agave speciation might be a result of their interaction. Further research on this topic could analyze the phylogenetic history and niche evolution in agaves and *Leptonycteris* bats to try to describe differences in their niche in the past. This information could then be projected to future scenarios to study potential trends in the niche evolution of these interacting species.

In Chapter III, I modeled the potential effects of global climate change on the potential distribution of the agave corridor and the pollinating bat *L. nivalis*. I found that the suitable areas for all of the *Agave* species analyzed and for the bat would retreat to higher elevation areas. Also, the overlap between agaves and the endangered pollinating bat will be reduced by at least 75%. Another consideration on the impacts of changing temperatures and precipitation is the effect on agave phenology. Although the specific cues that trigger agave flowering are not clearly understood, there is consensus that precipitation is an important variable. As a conclusion for Chapter III, I recommend implementing an annual monitoring program in the study area to document flowering timing in the agave populations and maintain a record precipitation data.

In Chapter IV, I analyzed the effects of three decades of land cover change on the potential area of distribution of *Agave* species occurring in the northern Mexican portion of the bat's range. I documented agave habitat loss and fragmentation trends in the region. I identified other potential threats in the region that were not possible to quantify for our analysis, including the effects of mining activities and wild fires. In conclusion, I

recommended implementing restoration activities of agave populations in depleted areas, for preventing further soil erosion in the short term and providing foraging resources for the endangered nectar-feeding bats in the long term.

The results of Chapter IV indicate that trends for agave habitat loss have slowed, but even under scenarios of no further habitat loss, climate change will continue to have impacts on the plant-pollinator interaction, as indicated in Chapter III.

During the summers of 2012, 2013 and 2014, I conducted field surveys in the study region. I was able to obtain new agave and *L. nivalis* locality data that was included in the models. Also I conducted vegetation quadrats to try to obtain indicators of the status of agave populations. These data are not yet sufficient for conducting statistical analysis and are not included in this dissertation. I recommend continuing with agave surveys in the region in order to gather sufficient information for statistical significant analysis that would provide insights on the agave population dynamics and trends. During my fieldwork, I developed working relationships with local conservation practitioners who are continuing with the surveys and bat monitoring, and have started activities to engage the local communities in the conservation efforts (Gomez-Ruiz et al. 2015).

Additionally, as a result of my field surveys, I started a collection of pollen found on the bat's hair. In collaboration with Dr. Vaughn Bryant, head of the Palynology laboratory in the Department of Anthropology, and his students, we started preliminary analysis of the pollen to identify the plant species. Preliminary results indicate that all of the pollen collected belongs to the genus *Agave*. This evidence emphasizes the

importance of agaves as the main food source for *L. nivalis* in northern Mexico. Further studies would try to identify the pollen to species level. Such information would help understand the use of the agaves by the bats and target populations of those agave species in conservation programs.

Overall, the studies in my dissertation contribute to understanding the impacts of global and regional environmental changes on the *Agave-L nivalis* corridor. The information obtained from my studies can help guide conservation activities and prioritize areas for the maintenance of this endangered corridor in the long term. Ultimately, my approach for analyzing the pollination corridor using ecological niche modeling and integrating scenarios of future climate and land cover change, can be broadly applied to inform conservation actions for other taxa.

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APPENDIX A

POTENTIAL DISTRIBUTION MAPS OF THE *Agave* SPECIES USING GARP AND MAXENT

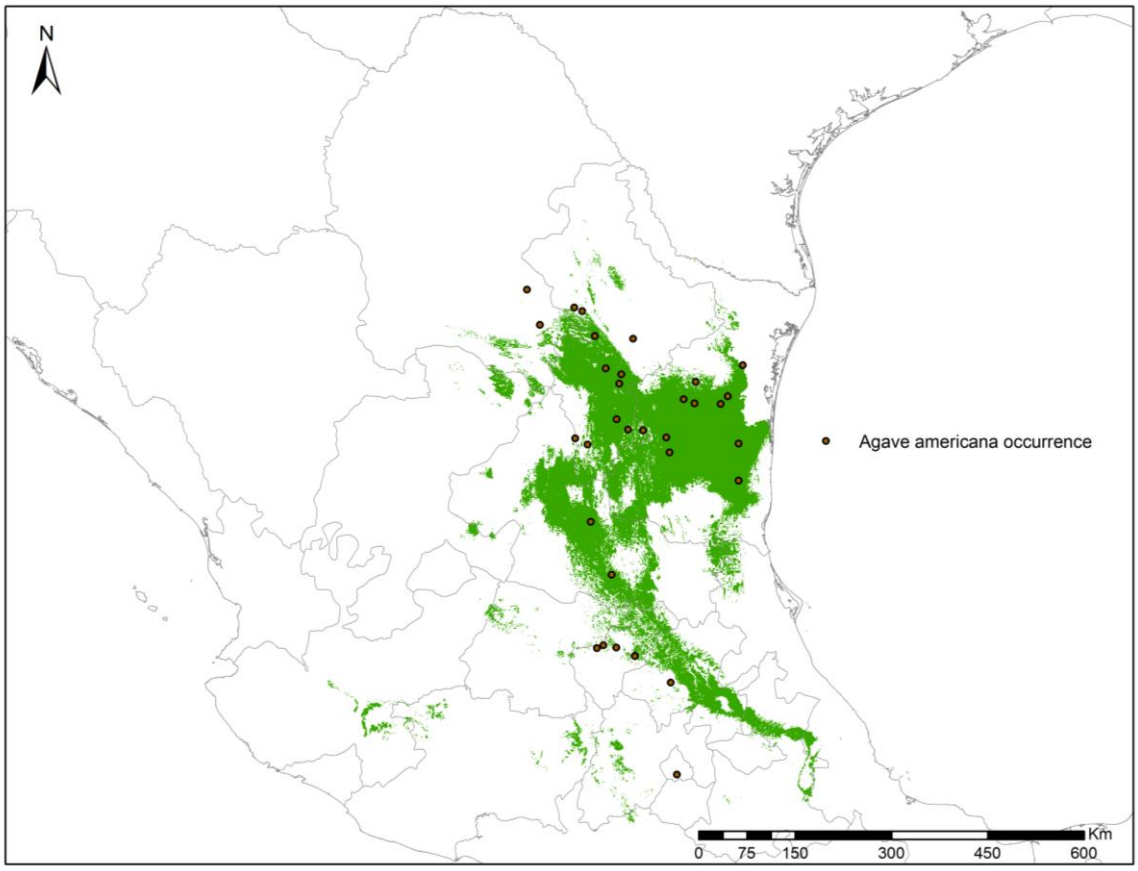


Fig. A1. Potential distribution model of *Agave americana*. Algorithm used: Maxent (partial AUC=1.67, threshold for binary output = 10 percentile training presence).

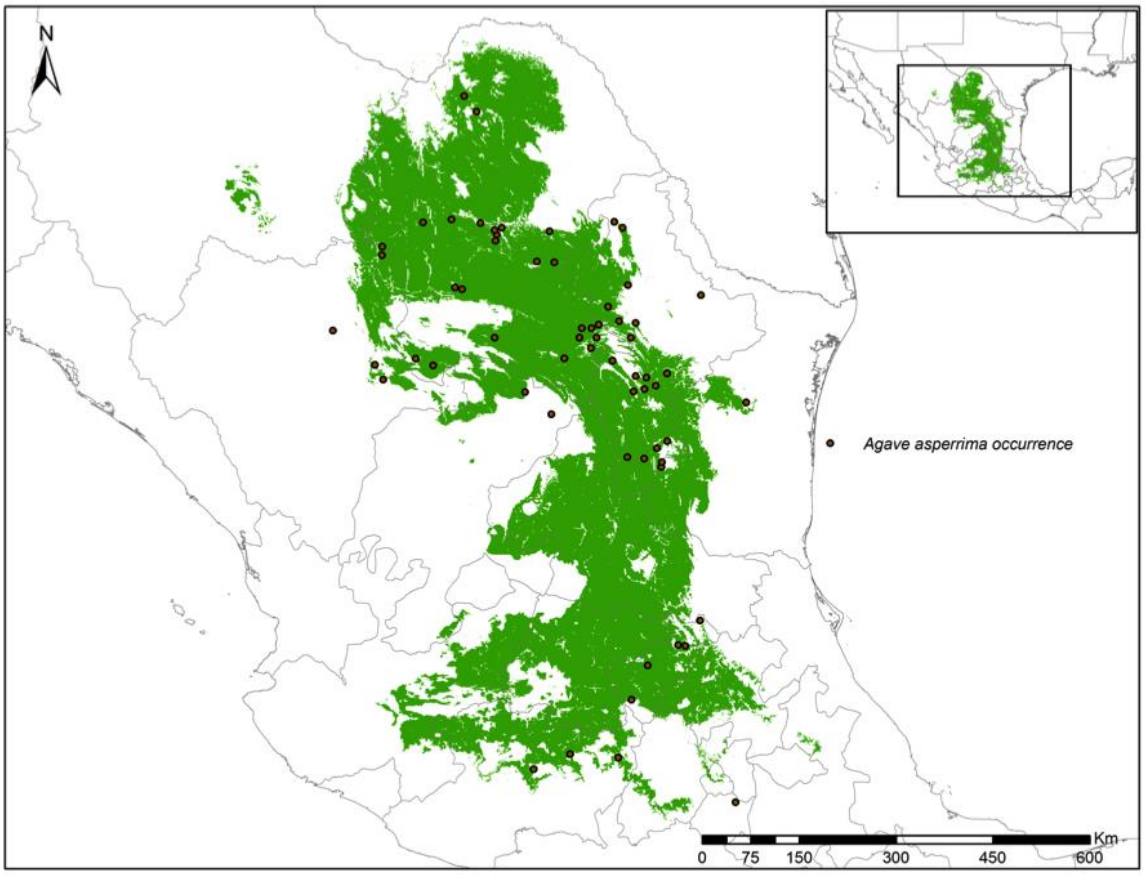


Fig. A2. Potential distribution model of *Agave asperrima*. Algorithm used: GARP (partial AUC=1.18, threshold for binary output = consensus area of best ten subsets).

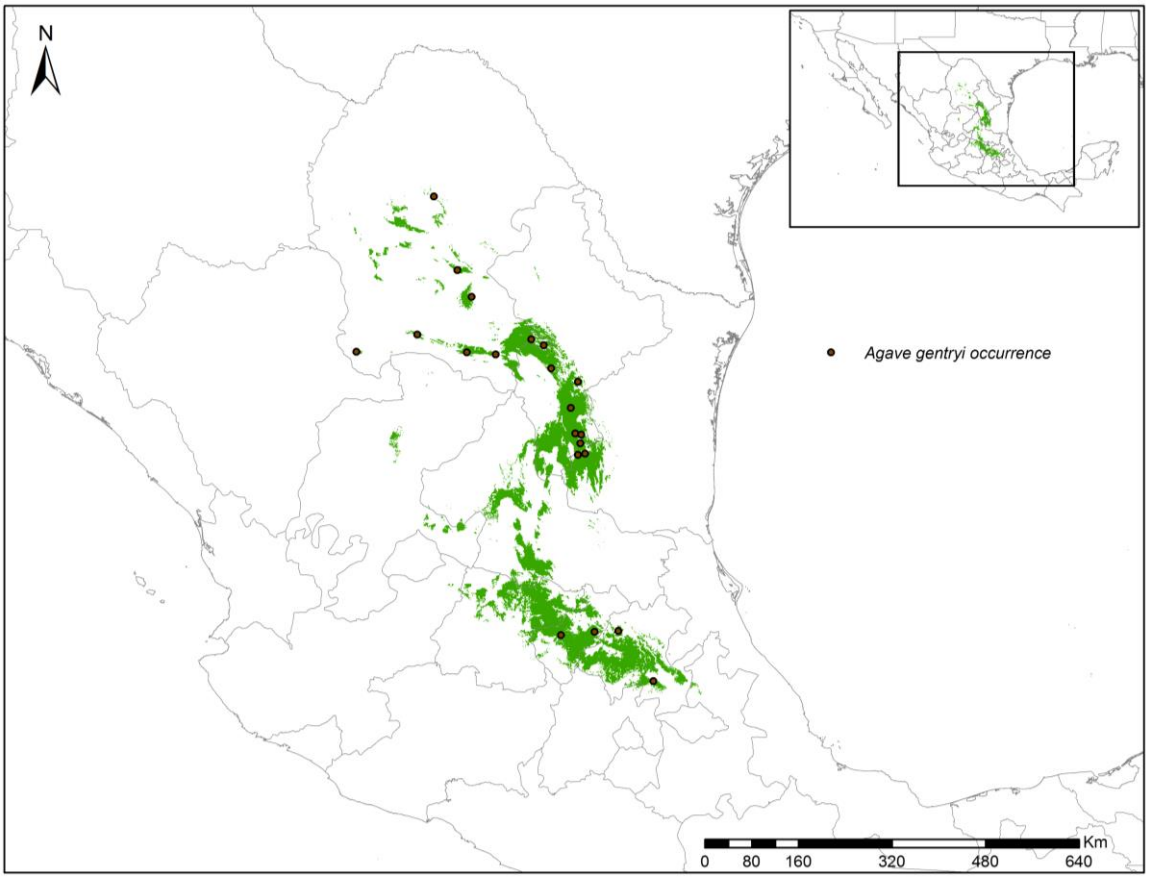


Fig. A3. Potential distribution model of *Agave gentryi*. Algorithm used: GARP (partial AUC=1.88, threshold for binary output = consensus area of best ten subsets).

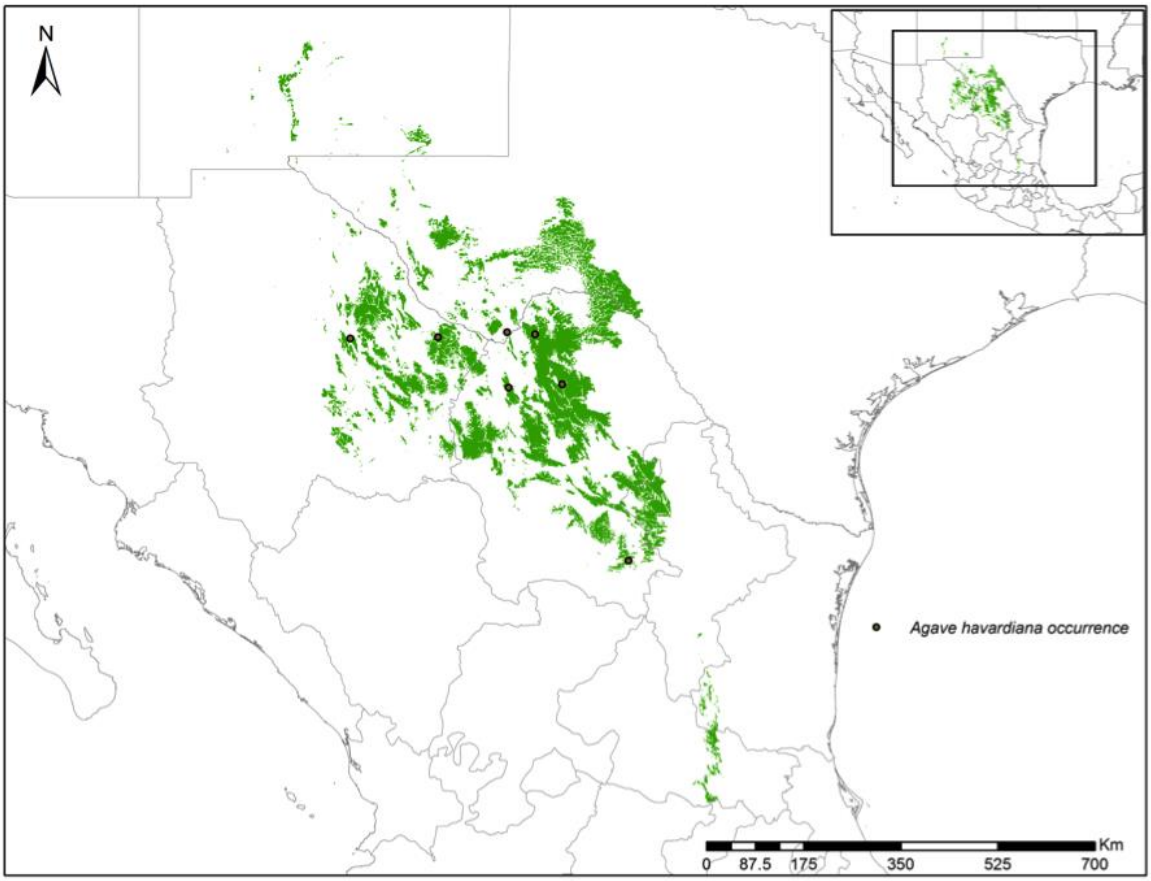


Fig. A4. Potential distribution of *Agave havardiana*. Algorithm used: Maxent (Jackknife performance evaluation = success rate 6/7, p-value: 0.026, threshold for binary output: 10 percentile training presence).

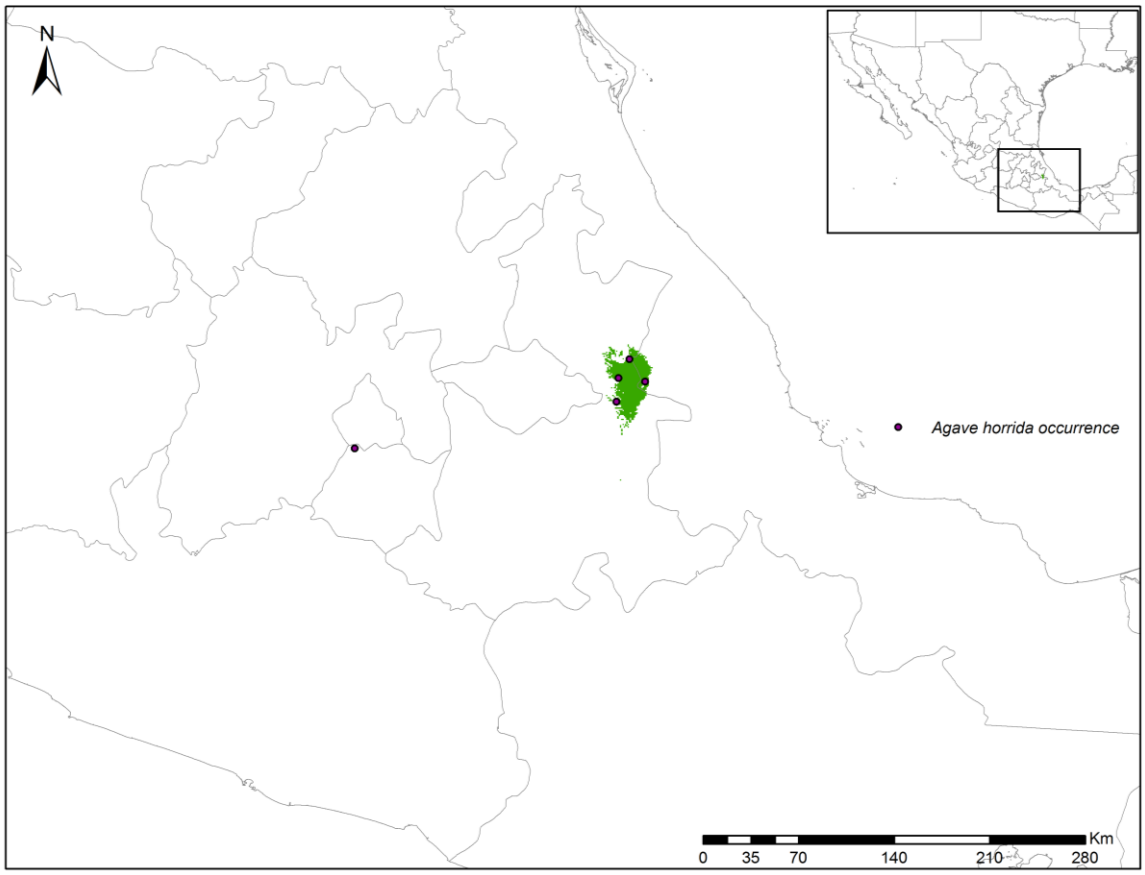


Fig. A5. Potential distribution of *Agave horrida*. Algorithm used: Maxent (Jackknife performance evaluation = success rate 2/5, p-value: 0.0003, threshold for binary output: 10 percentile training presence).

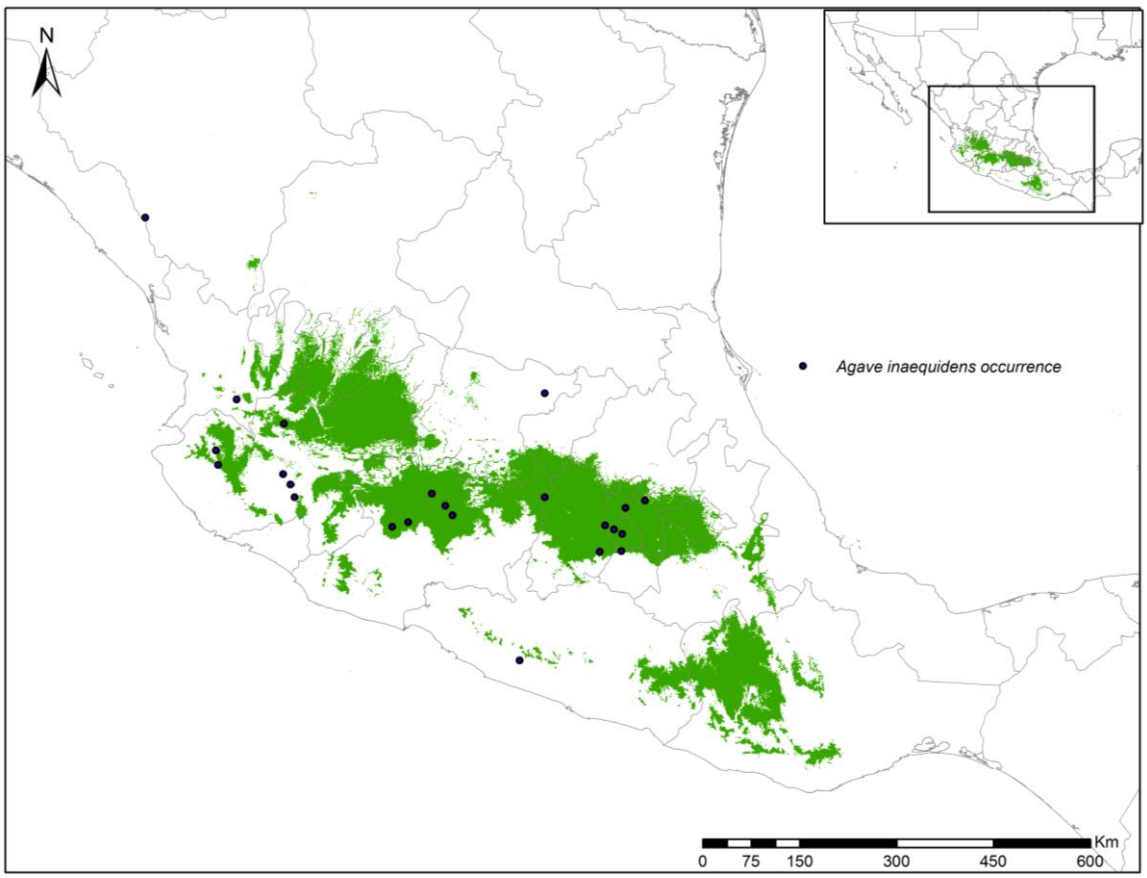


Fig. A6. Potential distribution of *Agave inaequidens*. Algorithm used: Maxent (partial AUC=1.56, threshold for binary output: 10 percentile training presence).

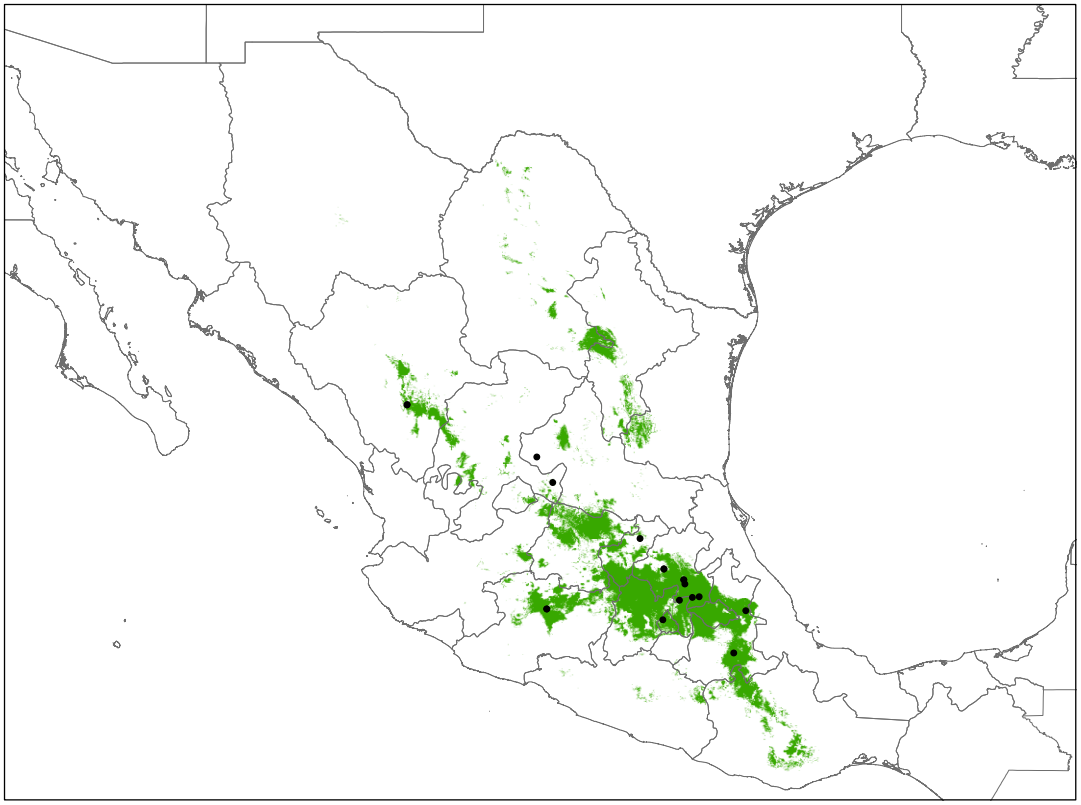

Fig. A7. Potential distribution of *Agave salmiana*. Algorithm used: Maxent (partial AUC=1.70, threshold for binary output: 10 percentile training presence).

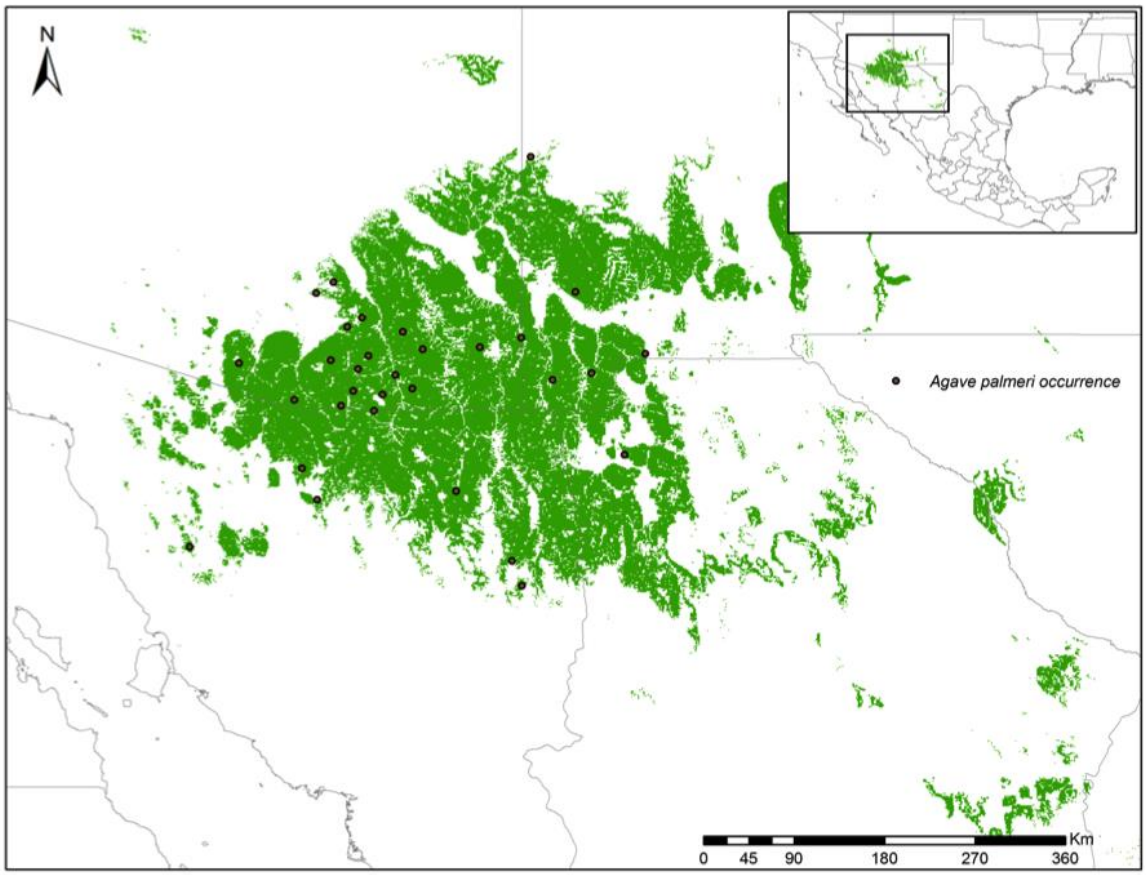


Fig. A8. Potential distribution of *Agave palmeri*. Algorithm used: Maxent (partial AUC=1.86, threshold for binary output: 10 percentile training presence).

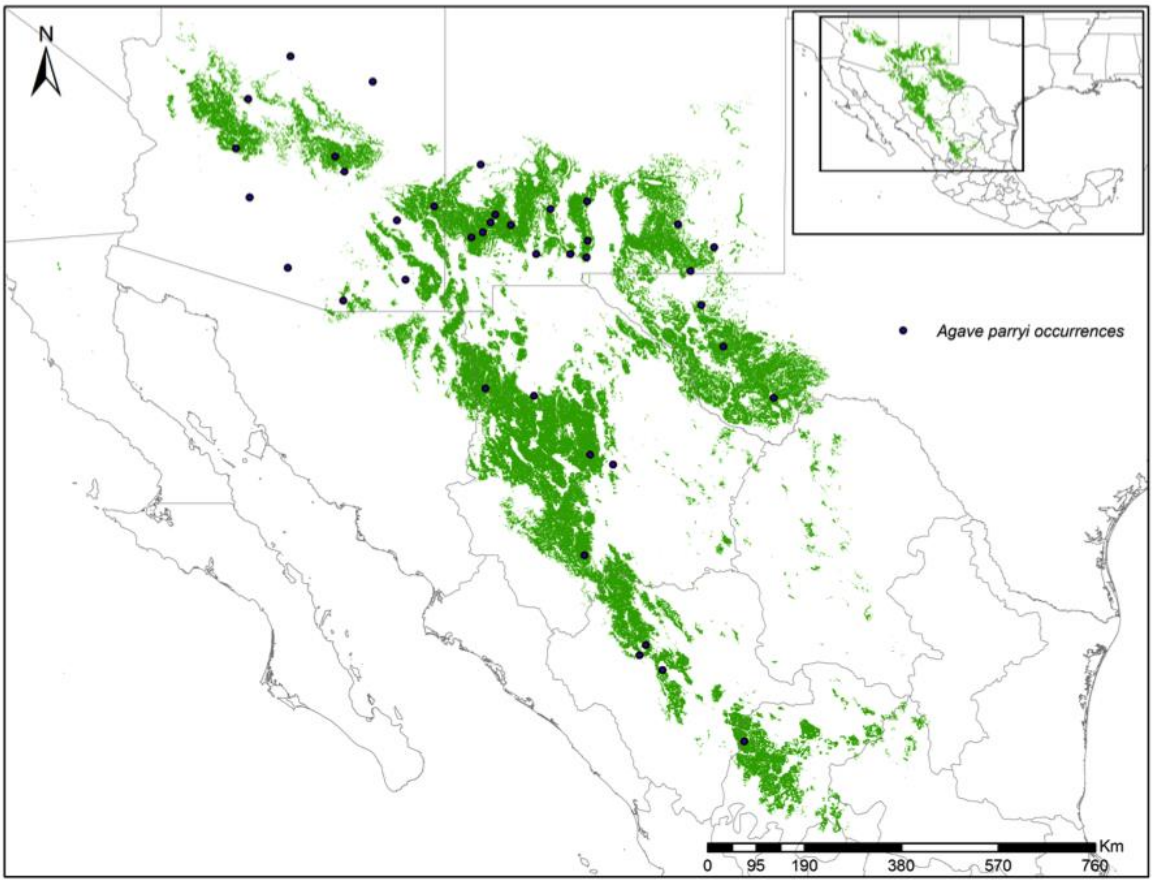


Fig. A9. Potential distribution of *Agave parryi*. Algorithm used: Maxent (partial AUC=1.39, threshold for binary output: 10 percentile training presence).

# APPENDIX B

## CLASSES INCLUDED IN INEGI LAND COVER MAPS

Table B1. List of land cover classes found in the study area in each INEGI map series. Class names are in the source language (Spanish). AA=Agriculture, BC=Conifer forest, BD=Deciduous forest, H2O=Water, NI=Other, SV=Bare ground, VM=Desert scrub, VP=Grassland, ZU=Human settlements

| New Class CODE | Serie I (1985) | Serie II (1993) | Serie III (2002) | Serie IV (2007) | Serie V (2011) |
|---|---|---|---|---|---|
| AA | 1. Temporal<br>2. Riego<br>3. Riego eventual<br>4. Riego suspendido<br>5. Humedad<br>6. Pastizal cultivado | 1. Temporal<br>2. Riego<br>3. Riego eventual<br>4. Riego suspendido<br>5. Pastizal cultivado | 1. Agricola-Pecuaria-Forestal | 1. Agricola-Pecuaria-Forestal | 1. Agricola-Pecuaria-Forestal |
| VM | 7. Matorral crasicaule<br>8. Matorral desertico microfilo<br>9. Matorral desertico rosetofilo<br>10. Matorral submontano<br>11. Chaparral | 6. Matorral crasicaule<br>7. Matorral desertico microfilo<br>8. Matorral desertico rosetofilo<br>9. Matorral submontano<br>10. Chaparral | 2. Matorral crasicaule<br>3. Matorral desertico microfilo<br>4. Matorral desertico rosetofilo<br>5. Matorral submontano<br>6. Chaparral | 2. Matorral crasicaule<br>3. Matorral desertico microfilo<br>4. Matorral desertico rosetofilo<br>5. Matorral submontano<br>6. Chaparral | 2. Matorral crasicaule<br>3. Matorral desertico microfilo<br>4. Matorral desertico rosetofilo<br>5. Matorral submontano<br>6. Chaparral |
| VP | 12. Pastizal natural<br>13. Pastizal inducido<br>14. Pastizal halofilo | 11. Pastizal natural<br>12. Pastizal inducido<br>13. Pastizal halofilo | 7. Pastizal natural<br>8. Pastizal inducido<br>9. Pastizal halofilo | 7. Pastizal natural<br>8. Pastizal inducido<br>9. Pastizal halofilo | 7. Pastizal natural<br>8. Pastizal inducido<br>9. Pastizal halofilo |
| BC | 15. Bosques de pino<br>16. Bosque de ayarin<br>17. Bosque de pino-encino | 14. Bosques de pino<br>15. Bosque de ayarin<br>16. Bosque de pino-encino | 10. Bosques de pino<br>11. Bosque de ayarin<br>12. Bosque de pino-encino | 10. Bosques de pino<br>11. Bosque de ayarin<br>12. Bosque de pino-encino | 10. Bosques de pino<br>11. Bosque de ayarin<br>12. Bosque de pino-encino |

Table B1 (Continued).

| New Class CODE | Serie I (1985) | Serie II (1993) | Serie III (2002) | Serie IV (2007) | Serie V (2011) |
|---|---|---|---|---|---|
| BD | 18. Bosque de galeria<br>19. Bosque de encino<br>20. Bosque de encino-pino | 17. Bosque de galeria<br>18. Bosque de encino<br>19. Bosque de encino-pino | 13. Bosque de galeria<br>14. Bosque de encino<br>15. Bosque de encino-pino | 13. Bosque de galeria<br>14. Bosque de encino<br>15. Bosque de encino-pino | 13. Bosque de galeria<br>14. Bosque de encino<br>15. Bosque de encino-pino |
| ZU | 21. Zona urbana | 20. Zona urbana | 16. Zona urbana<br>17. Asentamientos humanos | 16. Zona urbana<br>17. Asentamientos humanos | 16. Zona urbana<br>17. Asentamientos humanos |
| H2O | 22. Cuerpo de agua | 21. Cuerpo de agua | 18. Cuerpo de agua | 18. Cuerpo de agua | 18. Cuerpo de agua |
| SV | 23. Area sin vegetacion | 22. Area sin vegetacion | 19. Sin vegetacion aparente | 19. Sin vegetacion aparente<br>20. Desprovisto de vegetacion | 19. Sin vegetacion aparente<br>20. Desprovisto de vegetacion |
| NI | 24. Bosque bajo abierto<br>25. Bosque de oyamel<br>26. Bosque de tascate<br>27. Bosque mesofilo de montana<br>28. Huizachal<br>29. Matorral espinoso tamaulipeco | 23. Bosque bajo abierto<br>24. Bosque de oyamel<br>25. Bosque de tascate<br>26. Bosque mesofilo de montana<br>27. Huizachal<br>28. Matorral de coniferas | 20. Matorral espinoso tamaulipeco<br>21. Bosque mesofilo de montana<br>22. Matorral de coniferas<br>23. Bosque de tascate<br>24. Bosque de oyamel<br>25. Mezquital desertico | 21. Bosque de mezquite<br>22. Bosque de tascate<br>23. Bosque mesofilo de montana<br>24. Mezquital desertico<br>mezquital tropical<br>25. Pais extranjero | 21. Bosque de mezquite<br>22. Bosque de oyamel<br>23. Bosque de tascate<br>24. Bosque mesofilo de montana<br>25. Matorral de coniferas<br>26. Matorral espinoso tamaulipeco |

Table B1 (Continued).

| New Class CODE | Serie I (1985) | Serie II (1993) | Serie III (2002) | Serie IV (2007) | Serie V (2011) |
|---|---|---|---|---|---|
| NI | 30. Matorral subtropical | 29. Matorral espinoso tamaulipeco | 26. Mezquital tropical | 26. Palmar inducido | 27. Mezquital |
| | 31. Mezquital | 30. Matorral subtropical | 27. No aplicable | 27. Palmar natural | 28. Mezquital tropical |
| | 32. No aplicable | 31. Mezquital | 28. Palmar Inducido | 28. Pastizal gipsofilo | 29. Mezquital xerofilo |
| | 33. Pais extranjero | 32. No aplicable | 29. Palmar natural | 29. Pradera de alta montana | 30. Pais extranjero |
| | 34. Palmar | 33. Pais extranjero | 30. Pastizal gipsofilo | 30. Selva baja caducifolia | 31. Palmar inducido |
| | 35. Pastizal-huizachal | 34. Palmar | 31. Pradera de alta montana | 31. Selva baja espinosa caducifolia | 32. Palmar natural |
| | 36. Pastizal gipsofilo | 35. Pastizal-huizachal | 32. Selva baja caducifolia | 32. Selva baja subcaducifolia | 33. Pastizal gipsofilo |
| | 37. Selva baja caducifolia | 36. Pastizal gipsofilo | 33. Selva baja espinosa caducifolia | 33. Selva mediana subcaducifolia | 34. Selva baja caducifolia |
| | 38. Selva baja espinosa | 37. Pradera de alta montana | 34. Selva baja subcaducifolia | 34. Selva mediana subperennifolia | 35. Selva baja espinosa caducifolia |
| | 39. Selva baja subcaducifolia | 38. Selva baja caducifolia | 35. Selva mediana subcaducifolia | 35. Tular | 36. Selva baja subcaducifolia |
| | 40. Selva mediana subcaducifolia | 39. Selva baja espinosa | 36. Selva mediana subperennifolia | 36. Vegetacion de desiertos arenosos | 37. Selva mediana subcaducifolia |
| | 41. Selva mediana subperennifolia | 40. Selva baja subcaducifolia | 37. Tular | 37. Vegetacion gipsofila | 38. Selva mediana subperennifolia |
| | 42. Vegetacion de desiertos arenosos | 41. Selva mediana subcaducifolia | 38. Vegetacion de desiertos Arenosos | 38. Vegetacion halofila xerofila | 39. Tular |

Table B1 (Continued).

| New Class CODE | Serie I (1985) | Serie II (1993) | Serie III (2002) | Serie IV (2007) | Serie V (2011) |
|---|---|---|---|---|---|
| NI | 43. Vegetacion de galeria | 42. Selva mediana subperennifolia | 39. Vegetacion gipsofila | 39. Vegetacion halofila | 40. Vegetacion de desiertos arenosos |
| | 44. Vegetacion gipsofila | 43. Vegetacion de desiertos arenosos | 40. Vegetacion halofila hidrofila | 40. Vegetacion de galeria | 41. Vegetacion gipsofila |
| | 45. Vegetacion halofila | 44. Vegetacion de galeria | 41. Vegetacion halofila xerofila | | 42. Vegetacion halofila xerofila |
| | | 45. Vegetacion gipsofila | 42. Vegetacion de galeria | | 43. Vegetacion de galeria |
| | | 46. Vegetacion halofila | 43. Pais extranjero | | |

APPENDIX C

GEOGRAPHIC DISTRIBUTION OF AREAS GAINED AND LOST IN DESERT SCRUB, CONIFER AND DECIDUOUS FOREST

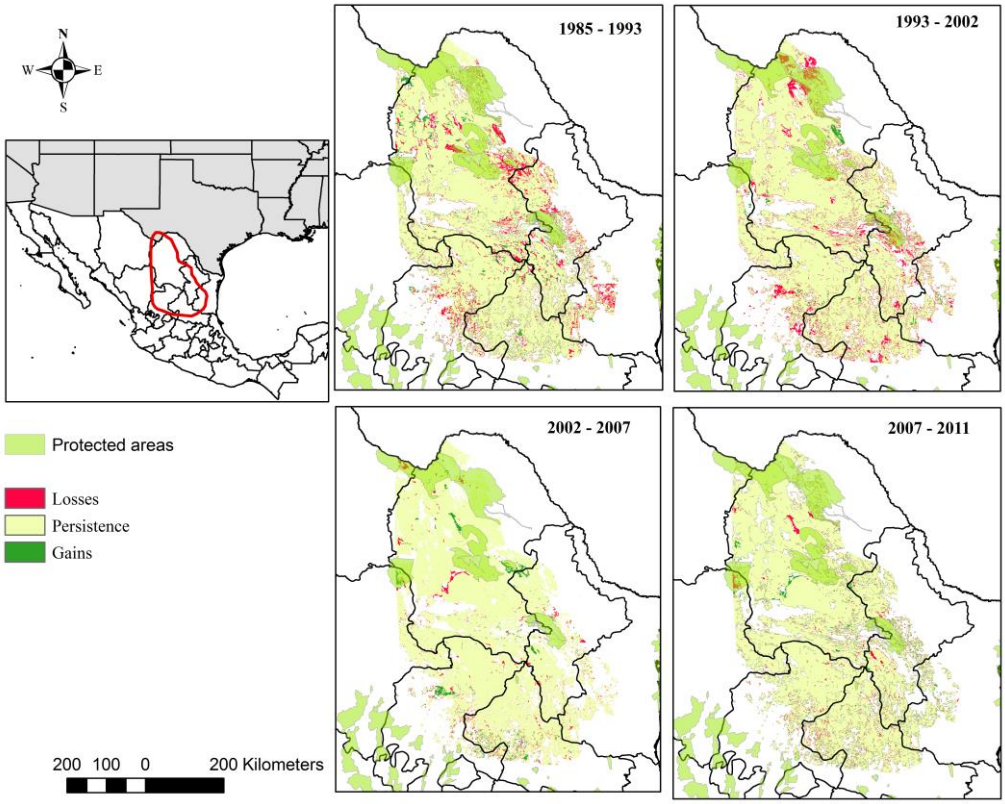


Fig. C1. Distribution of area gain (green) and loss (red) in desert scrub.

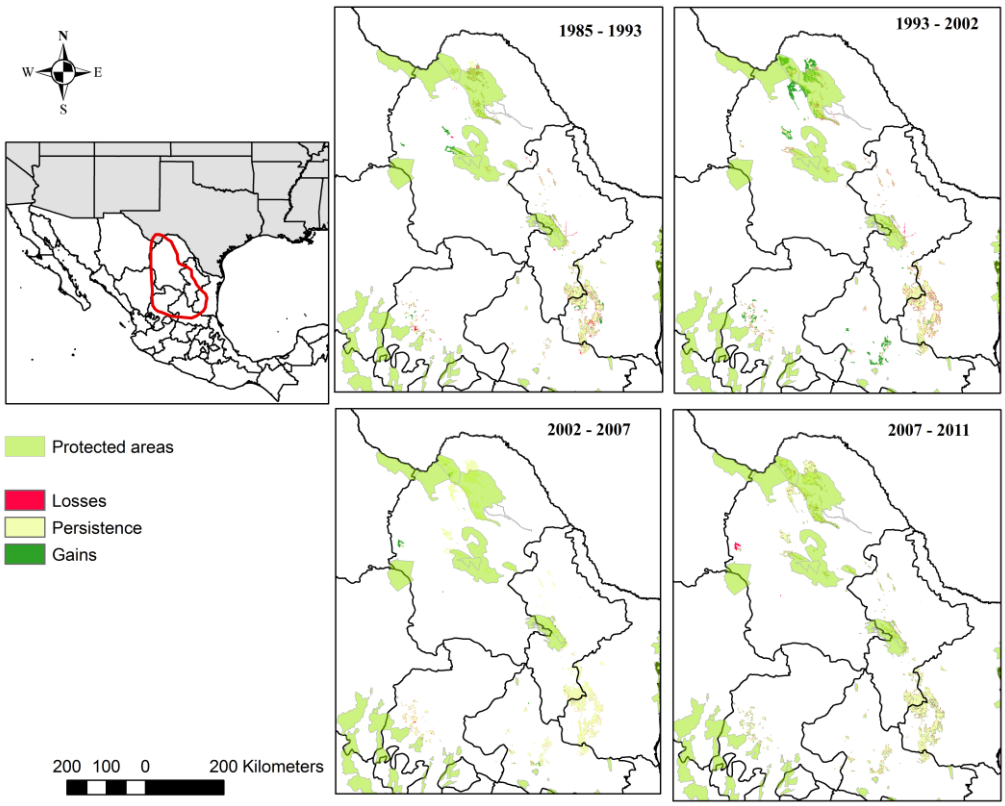


Fig. C2. Distribution of area gain (green) and loss (red) in deciduous forest.

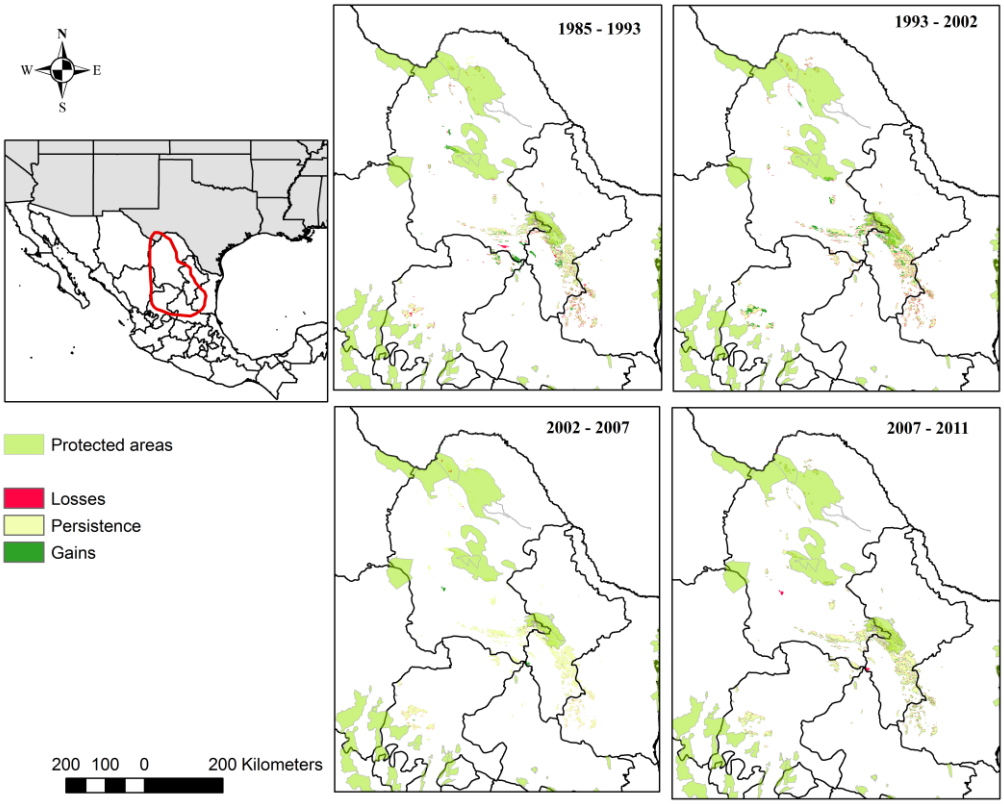


Fig. C3. Distribution of area gain (green) and loss (red) in conifer forest.

APPENDIX D

CONTRIBUTIONS TO NET CHANGE IN CONIFER AND DECIDUOUS FOREST

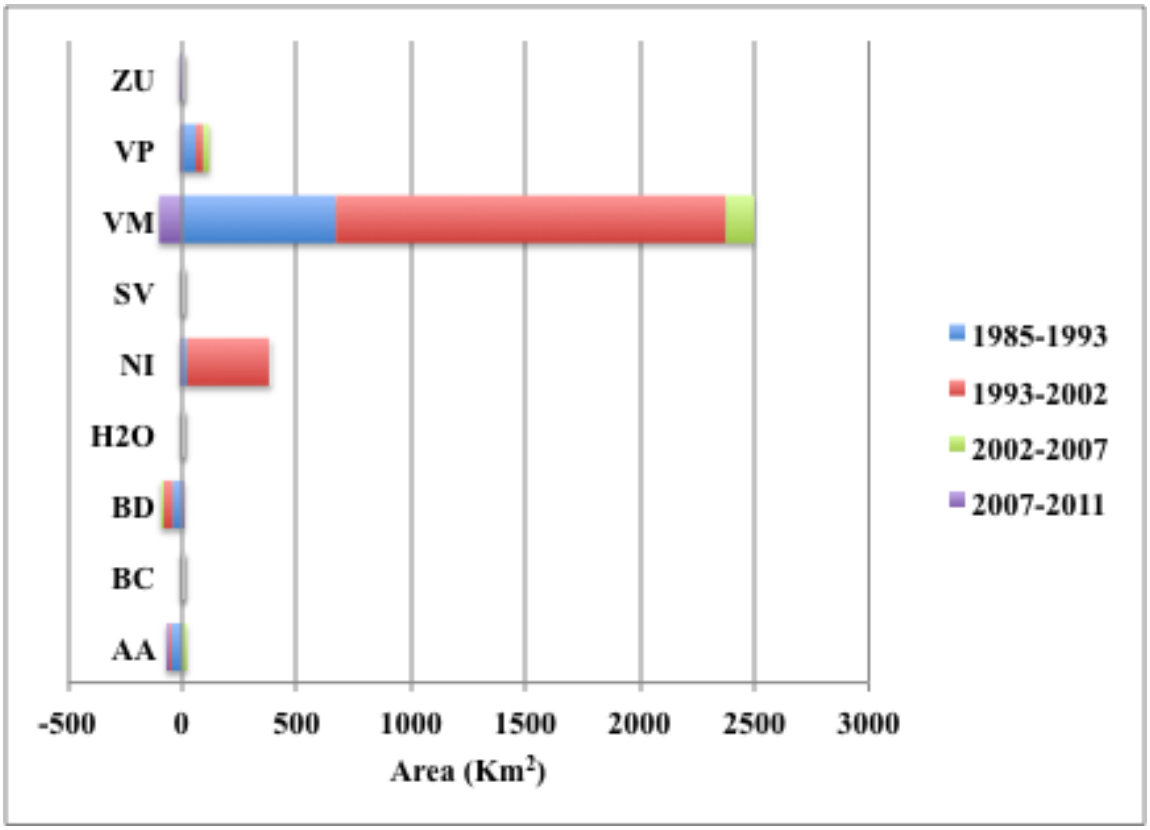


Fig. D1. Contributions to net change in conifer forest. AA=Agriculture, BC=Conifer forest, BD=Deciduous forest, H2O=Water, NI=Other, SV=Bare ground, VM=Desert scrub, VP=Grassland, ZU=Human settlements.

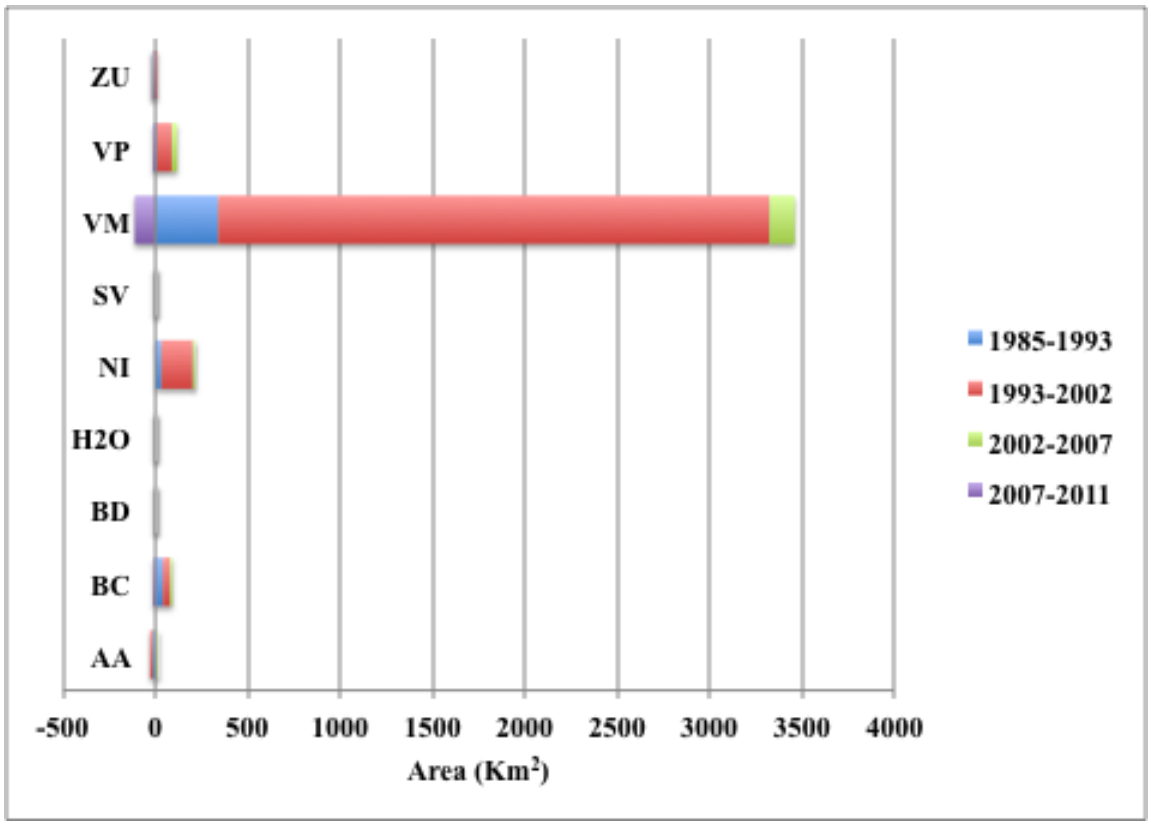


Fig. D2. Contributions to net change in deciduous forest. AA=Agriculture, BC=Conifer forest, BD=Deciduous forest, H2O=Water, NI=Other, SV=Bare ground, VM=Desert scrub, VP=Grassland, ZU=Human settlements.

APPENDIX E

PERCENT CHANGE IN AREA GAINS AND LOSSES PER CLASS

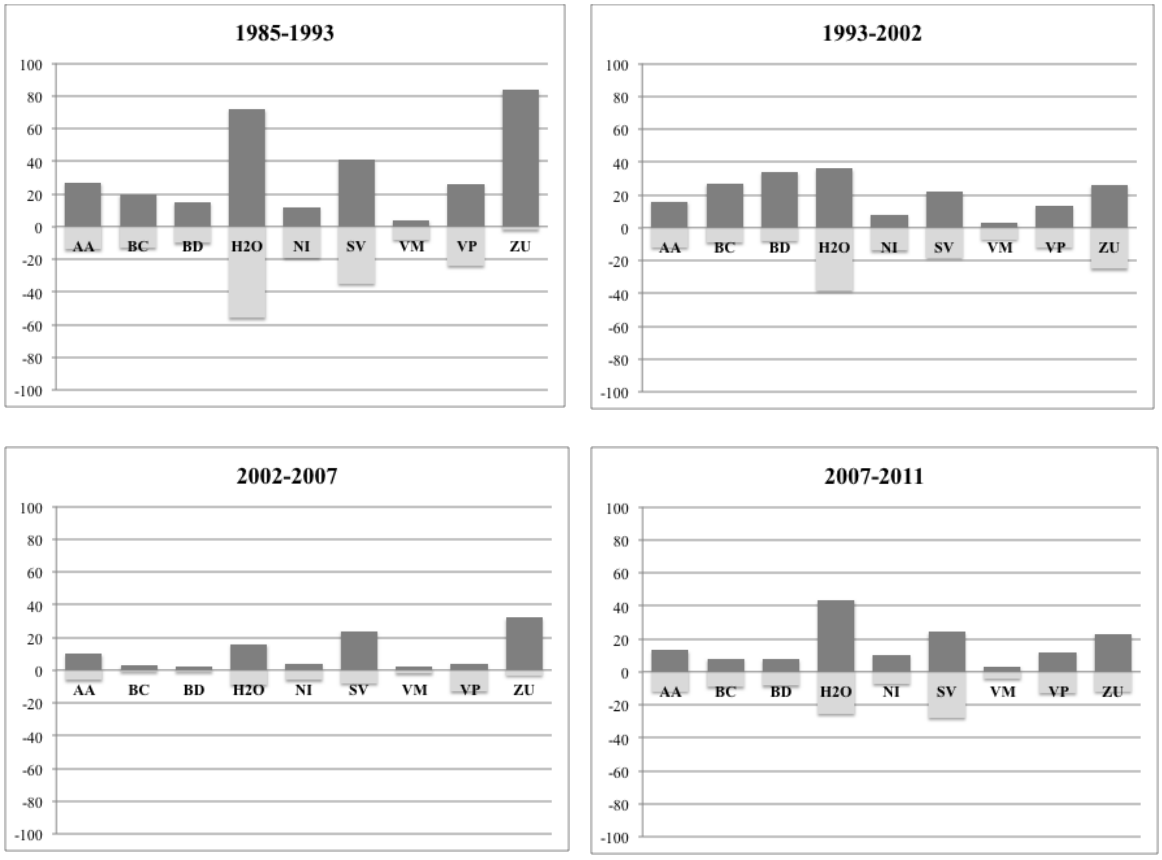


Fig. E1. Percent change in gains (dark grey) and losses (light grey) per class. AA=Agriculture, BC=Conifer forest, BD=Deciduous forest, H2O=Water, NI=Other, SV=Bare ground, VM=Desert scrub, VP=Grassland, ZU=Human settlements
*Percent Change = (# Pixels changed for a class / area of a class in the later land cover image)*100

APPENDIX F

AVAILABLE AGAVE HABITAT BY 2011 IN THE STUDY REGION

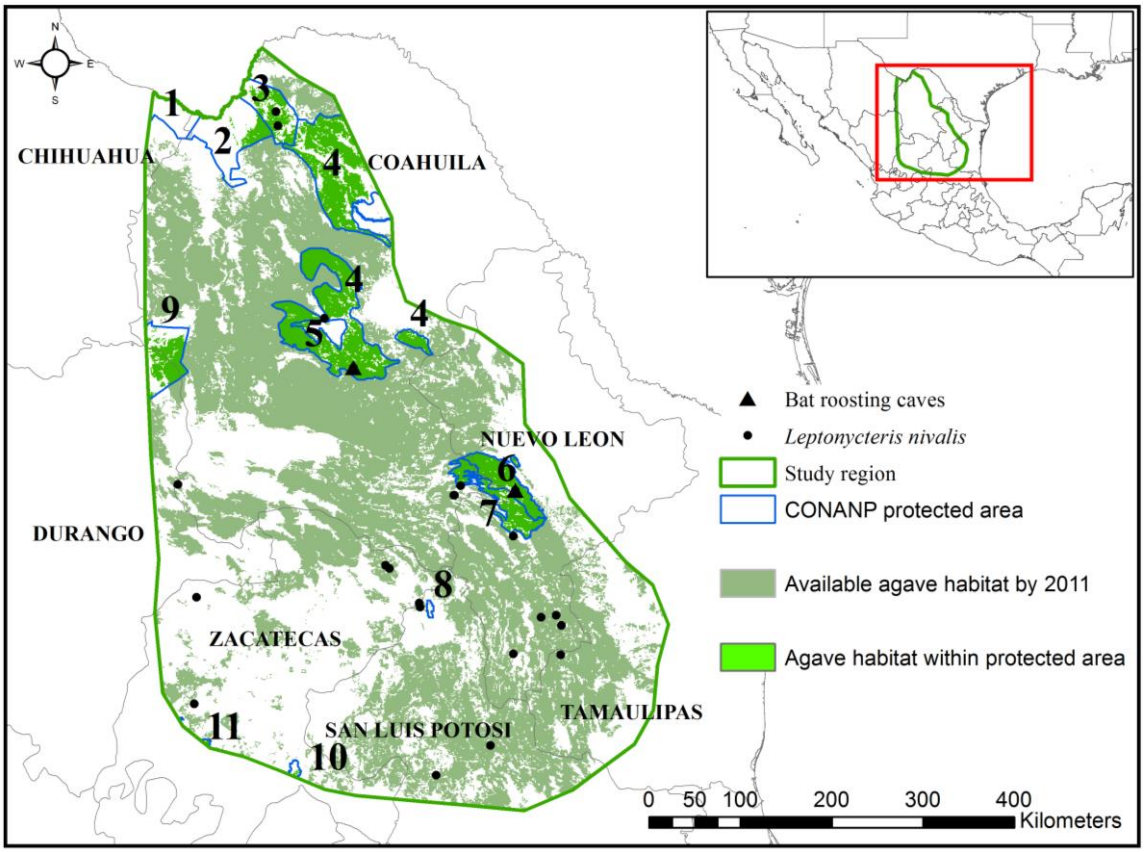


Fig. F1. Available agave habitat by 2011 in the study region. The numbers indicate the protected areas designated by Mexico's commission on protected areas (CONANP): 1. Cañon de Santa Elena, 2. Ocampo, 3. Maderas del Carmen, 4. CADNR 04 Don Martin, 5. Cuatrocienegas, 6. Cumbres de Monterrey, 7. CADNR 26 Bajo Rio San Juan, 8. Sierra la Mojonera, 9. Mapimí, 10. CADNR 01 Pabellon